

Original research article

Response of *Abies spectabilis* from the treeline ecotone to climate change in Mustang region of Nepal Himalayas

Narayan Prasad Gaire^{a*}, Yub Raj Dhakal^{a,b*}, Shravan Ghimire^{b,c}, Sanjaya Bhandari^b, Srijan Poudel^b, Santosh K. Shah^d

^a Department of Environment Science, Patan Multiple Campus, Tribhuvan University, Patan Dhoka, Lalitpur, Nepal

^b Siddhartha Environmental Services, Kathmandu, Nepal

^c Institute of Mountain Hazard and Environment, Chinese Academy of Sciences, Chengdu, China

^d Birbal Sahni Institute of Paleosciences, Lucknow, India

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ABSTRACT

Alpine treelines serve as a sensitive bio-monitor and an early warning indicator of climate change impacts on high-altitude ecosystems. We conducted a dendrochronological study in the treeline ecotones in the Mustang region, Annapurna Conservation Area, Nepal, to assess the effects of climate change on *Abies spectabilis* (D. Don) Mirb. We collected tree core samples from 40 trees and analysed them, using the standard dendrochronological procedure. We developed a 97-year tree-ring width chronology spanning from 1919 to 2015, which demonstrates strong dendroclimatic potential. The sampled trees had an average annual radial growth of 0.37 ± 0.74 mm/yr and a mean age of 43.1 years. The basal area increment (BAI) chronology of this species in this region indicates a slight decline in its growth in recent years. Moisture availability during the growing season primarily controls the growth of *A. spectabilis*, as indicated by its negative relationship with summer maximum temperature and positive relationship with precipitation. A higher winter maximum temperature also positively favoured the growth in the following growing season. These climatic influences have shifted over time, with increasingly negative relationships with June and August temperatures and a weakened positive relationship with July temperatures, while the positive influence of August precipitation remains stable. The projected increases in drought frequency and severity under ongoing global warming are likely to adversely affect the growth of *A. spectabilis* at high-elevation treelines.

INTRODUCTION

Nepal Himalayas are experiencing rapid climate change and increasing climatic extremes, which are adversely affecting multiple sectors (DHM, 2017; Karki et al., 2017; MoFE, 2021a, b; Chaudhary et al., 2023; ICIMOD, 2023). Researchers consider the alpine treeline ecotone a highly sensitive bioindicator and bio-monitor of climate change impacts on high-mountain plant communities (Körner, 2012; Lu et al., 2025). Treeline shift, an influence of climate change, has been reported from various parts of the world with varying rates at different sites (Lu et al., 2025). Trees in the alpine treeline ecotone often respond to climate

change through changes in demography, regeneration patterns, growth rates, growth forms, and the position of the treeline itself (Körner, 2012; Sigdel et al., 2018, 2024; Gaire et al., 2023a; Lu et al., 2025). Temperature and moisture balance are two significant factors that influence treeline formation and drive large-scale ecological changes (Lu et al., 2025). Situated in the central part of the Himalayas, Nepal provides an opportunity to investigate the response of treeline to climate change. Three to four species often form the treeline ecotone in the Nepal Himalayas, although monospecific treelines also occur (Gaire et al., 2023a). Studies from the Nepal Himalayas have shown stable to changing treeline positions, increasing regeneration

* Corresponding authors: Equal level of contribution and correspondence:
 E-mail address: narayan.gaire@pmc.tu.edu.np; dhakalyr@gmail.com

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and varying tree growth rates in response to recent climate change (Tiwari et al., 2017a; Sigdel et al., 2018, 2024; Pandey et al., 2020; Panthi et al., 2020; Gaire et al., 2023a, b).

The trans-Himalayan region is considered one of the most climate change-sensitive areas and is an important Himalayan biodiversity hotspot and, therefore, an ideal place to study the impacts of climate change (Aryal et al., 2018; Bhadra et al., 2021; ICIMOD, 2023; Adhikari et al., 2024). Manang and Mustang districts in Nepal typically represent the physiographic characteristics and climate of the trans-Himalayan region. Mustang is rich in biological and cultural diversity and is a famous tourist destination, particularly the Annapurna Conservation Area (ACA) (DNPWC, 2019). However, the area has been witnessing rapid climate change, increasing extremes and ensuing disasters in recent years with adverse impacts on its biophysical and socioecological systems (Fort, 2014; Aryal et al., 2017; Bhadra et al., 2021; Hamal et al., 2022; Sigdel et al., 2022; Adhikari & Mathema, 2023; Adhikari et al., 2024; Ghimire et al., 2025). The region recently experienced extreme floods, which damaged infrastructure and threatened local livelihoods (Fort et al., 2024), for example, the Kagbeni flood in August 2023 and the glacial lake outburst flood (GLOF)-induced flood in Chumjung, Upper Mustang, in July 2025. At the same time, prolonged drought-associated drying of water sources has severely affected agriculture and other livelihood options. This ultimately leads to abandonment of settlements and migration of communities from villages, as has happened as Dhye and Samjong villages (Poudel & Duex, 2017; Sherchan, 2019; Bhadra et al., 2021). These climatic extremes are adversely affecting the livelihoods of the local people (Aryal et al., 2017). Mustang lies in one of the driest regions of Nepal, and, hence, offers a unique opportunity to assess how forest vegetation responds to the warming and drying conditions in the future (MOFE, 2021a; IPCC, 2022). However, there are limited studies on the impacts of climate change on forests and biodiversity sectors of the region (Meier et al., 2022; Ghimire et al., 2025). Among the several approaches used to assess the impacts of climate change on forest vegetation in the treeline ecotone, such as repeat monitoring of permanent plots, remote sensing, vegetation surveys and tree rings, the tree-ring methods are the most widely used (Speer, 2010; Körner, 2012; Lu et al., 2025). Therefore, we conducted the present dendrochronological study in the Mustang region.

Study of tree rings offers a wide range of applications, including assessment of the climate sensitivity and vulnerability of species to climate change (Fritts, 1976; Speer, 2010). Tree rings provide exceptionally valuable paleoclimatic information across spatial scales, ranging from a few hectares to entire hemisphere and across temporal scales, spanning, such as ice-storms, to decades of droughts and centuries of shifts in changed global atmospheric circulation (Fritts, 1976; Cook et al., 2003; PAGES 2k Consortium, 2013). They have been extensively used to investigate treeline dynamics, reconstruct past climate, analyse long-term forest growth, forecast future growth, examine forest health and support archaeological studies, among

other applications (Speer, 2010; Camarero et al., 2021; Aryal et al., 2023).

The Mustang region hosts several promising tree species for dendrochronological research, and previous dendrochronological studies in the region have examined *Abies spectabilis*, *Betula utilis*, *Juniperus* spp. and *Pinus wallichiana* (Cook et al., 2003; Kharal et al., 2014; Tiwari et al., 2017a, b; Brunello et al., 2019; Gautam et al., 2020). *Abies spectabilis* (D. Don) Mirb., also known as the Himalayan Silver Fir, a Himalayan native species, is highly sensitive to climate change (Gaire et al., 2023a). Researchers have also utilized tree-ring studies in the Mustang region to investigate settlement history and to date ancient structures in the region, such as a historical palace (Schmidt, 1992; Schmidt et al., 1999; Gmińska-Nowak & Waźny, 2020). A treeline dynamics study from Mustang reported the gradual upward shift of *A. spectabilis* in the treeline ecotone (Tiwari et al., 2017a). Furthermore, recent growth decline in another treeline-forming species, *Betula utilis*, has been reported (Tiwari et al., 2017b). However, studies evaluating long-term growth and climate sensitivity of *A. spectabilis* using basal area increment (BAI) in the treeline ecotone remain limited, and we did not find any published literature on BAI studies for this species from the Mustang region. In other parts of the Nepal Himalayas, BAI studies on *A. spectabilis* in the treeline ecotone have reported both increase and decrease in growth consequent to climate change (Panthi et al., 2020; Camarero et al., 2021; Gaire et al., 2023b). This study aims to develop a tree-ring width and BAI chronology of *A. spectabilis* to assess its long-term growth pattern and climatic responses, along with the temporal stability of growth-climate relationships. The finding of this study will provide an important reference for understanding the climatic sensitivity and growth dynamics of *A. spectabilis* in the context of rapid climate change in Nepal.

MATERIALS AND METHODS

Study area and climate

The study area is located in Mustang District (Figure 1), which is part of the ACA (DNPWC, 2019). The southern part of the district supports diverse vegetation, dominated by *Tsuga dumosa*, *Pinus wallichiana*, *Abies spectabilis* and Juniper species. In contrast, the northern and trans-Himalayan zones are characterized by xerophytic *Caragana gerardiana* steppe with occasional *Juniperus indica* (DNPWC, 2019). The northern Mustang, situated beyond the orographic barrier, experiences semi-arid conditions, with strong winds and high solar radiation (Brunello et al., 2019).

The climate of the region is influenced by the Indian summer monsoon, westerlies and strong orographic effects. Majority of the annual precipitation is received during the monsoon season, but the percentage share in annual total rainfall is less compared to the stations situated in the southern slope of the Himalayas (DHM, 2017). The northern part of the Mustang district receives very low annual rainfall because it lies in the rain shadow zone of Dhaulagiri, Nilgiri and Annapurna mountains. Winters are extremely

cold, with snowfall and frequent frost events during December–February (Figure 2a). The climate data analysis from the Jomsom meteorological station (1982–2014) indicates a mean annual total rainfall of 265 mm. Over this period, the station recorded a slight but statistically non-significant increasing trend in annual rainfall (2.0 mm/yr; $n = 33$, $R = 0.24$, $p > 0.05$) (Figure 2d). However, both annual mean temperature (0.034 °C/yr) and annual minimum temperature (0.064 °C/yr) exhibit significant increasing trends (Figure 2b and 2c).

Tree-core collection and analysis

In the present study, an anthropogenically least-disturbed *Abies* treeline site was selected for sample collection. Tree-core samples were collected from Yak Kharka (foothills of Dhaulagiri Mountain) and the Kosari region (foothills of Nilgiri Mountain). All the samples were collected from the treeline ecotone at approximately 4,000 masl by using an increment borer (Haglof, Sweden), following the standard dendrochronological procedures (Fritts, 1976; Cook & Kairiukstis, 1990; Speer, 2010). One to two cores per tree were collected from each tree, depending on the suitability of the tree for core collection. All collected cores were packed in plastic straw pipes, labelled and transported to the Dendro laboratory of the Forest Research and Training Centre (FRTC), Kathmandu, and Nepal Academy of Science and Technology (NAST), Lalitpur, for further processing and analysis.

In the laboratory, collected cores were airdried for a few days and mounted on wooden frames using adhesive glue, with the transverse surface of the core facing upwards, and again left for drying up of the glue for a few days. After airdrying of glue, the surface of each core was progressively sanded and polished using increasing finer grades of sandpaper (100 to 1000 grits) until annual ring boundaries were clearly visible under a stereozoom microscope. Each ring of every sample was counted and assigned to a calendar year based on the known outer ring for the sampling year. Cross-dating was carried out to verify the accuracy of the calendar dates assigned to each ring of the sample (Fritts, 1976; Speer, 2010). The width of each ring was measured to the nearest 0.01 mm precision using a LINTAB5™ measuring system attached to a computer with the TSAP-Win software package (Rinn, 2003). All tree-ring series were visually cross-dated by matching the patterns of wide and narrow rings to account for the possibility of ring-growth anomalies, such as missing or false rings or measurement error (Fritts, 1976; Speer, 2010). Additionally, each tree-ring width series was verified statistically by looking Gleichläufigkeit, t -values and the cross-date index (CDI) using the software package TSAP-Win (Rinn, 2003). The accuracy of cross-dating and measurements was further checked using COFECHA, a quality control program (Holmes, 1983). Cores that showed poor correlation in COFECHA or had several breakages

and very young samples were excluded from the final dataset prior to chronology development.

Standardization and chronology development

The corrected ring-width data were standardized using the computer programs, RCSigFree (Melvin & Briffa, 2008; <http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>) and the *dplR* package in R environment (Bunn, 2008). The standardization process was applied to remove geometric and ecological growth trends associated with the tree-to-tree competition and stand dynamics, while preserving variability related to climate (Cook & Kairiukstis, 1990; Bunn, 2008). The ring-width series were standardized using an appropriate negative exponential, linear regression, or age-dependent cubic spline, depending on the characteristics of each series. After detrending, the individual standardized series were averaged using a bi-weight robust mean function (Bunn, 2008) to develop a site chronology. Various chronology statistics, like mean sensitivity, standard deviation, autocorrelation, within-tree correlation, between-tree correlation, mean series correlation, signal-to-noise ratio (SNR), expressed population signal (EPS) and variance explained, were calculated to assess the quality of the site chronologies (Briffa, 1995; Wigley et al., 1984). To assess the long-term growth of the trees, the raw tree-ring width measurements were converted into BAI using the “*bai.out*” function in the *dplR* package (Bunn, 2008), and a BAI chronology was subsequently developed.

Tree-growth climatic relationship

Climatic data from the nearest meteorological stations were collected from the Department of Hydrology and Meteorology (DHM), Kathmandu, for all available years and analysed. Missing values in the station datasets were computed by the average value of the same months' data and used in the response function analysis. Because climate in the preceding growing season often influences tree growth in the following year (Fritts, 1976), we analysed the effects of temperature and precipitation from September of the previous growth year to October of the current growth year. Similarly, seasonal climate responses were evaluated for the three major seasons that are commonly used in Nepal: winter (December–February), spring (March–May) and summer (June–September) (DHM, 2017). The relationships between the standard tree-ring width chronology and climatic variables: average (T_{\min} = minimum, T_{\max} = maximum, T_{mean} = mean) temperatures and the total precipitation were analysed by using bootstrapped correlation functions available in the “*treeclim*” R package (Zang & Biondi, 2015). Temporal stability of the growth-climate response was assessed by using moving correlation analysis, also performed with the “*treeclim*” R package (Zang & Biondi, 2015).

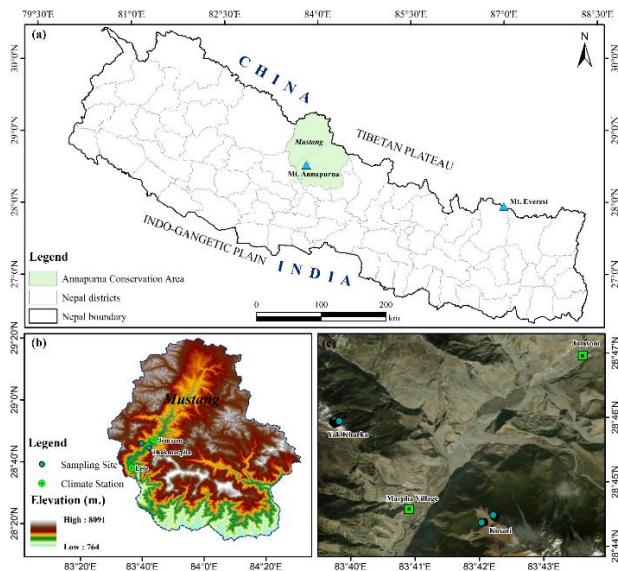


Figure 1 Location map of study area showing (a) Mustang district and Annapurna Conservation Area, (b) sampling sites and climatic stations in digital elevation model in Annapurna Conservation Area, and (c) sampling sites and major settlements

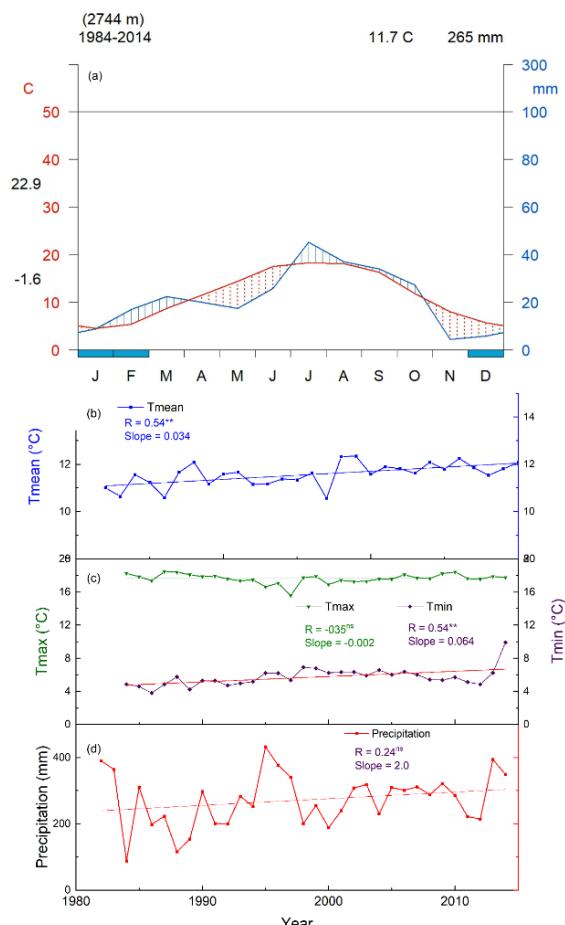


Figure 2 Umbro thermic graph of Mustang region (a) and annual climatic trend (temperature and precipitation) in the study area in Mustang (b-d). The “**” symbol indicates a significant trend in climate data while “ns” indicates a non-significant trend.

RESULTS

Tree-ring chronology and long-term growth of *Abies spectabilis* in the treeline region

The analysis of 2,114 annual rings from over 40 trees indicated that the mean radial growth of *A. spectabilis* in the treeline ecotone in the Mustang region was 0.37 ± 0.74 mm/yr, with an average tree age of 43.1 years. From the study, a 97-year tree-ring width chronology spanning from 1919 to 2015 was developed using 32 cross-dated samples, revealing distinct periods of enhanced and reduced growth (Figure 3). A slight growth increase was observed after the 1970s. The ring-width chronologies showed a dendroclimatic potential, characterized by a high expressed population signal (EPS), moderate mean sensitivity (0.224) and series intercorrelation (R-bar = 0.509) (Figure 3). Tree-ring chronology after 1949 is reliable as it crosses the commonly used EPS threshold value of 0.85 in that year.

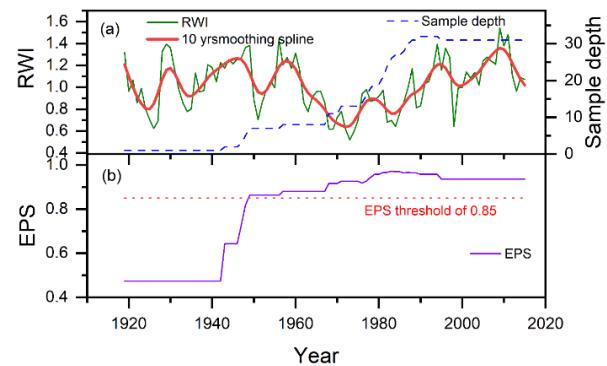


Figure 3 Tree-ring width chronology of *Abies spectabilis* from Mustang, along with sample depth (a) and running EPS (b)

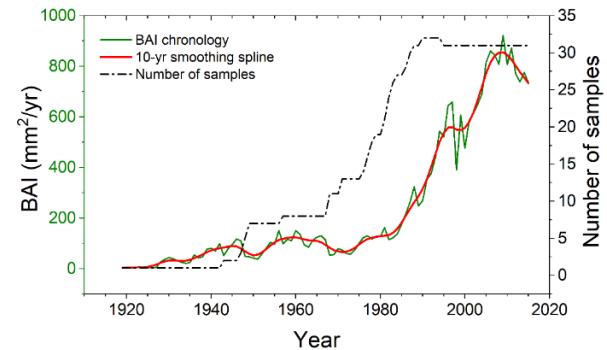


Figure 4 Basal area increment (BAI) chronology of *Abies spectabilis* from Mustang (green line), along with 10-year smoothing spline of BAI (red thick line) and sample depth (dotted line)

The BAI chronology further indicated that *A. spectabilis* in the treeline ecotone was relatively young and in an active phase, exhibiting an overall positive growth trend over time (Figure 4). However, a slight decline in BAI was observed in recent years (Figure 4).

Climatic influence in the growth of *Abies spectabilis* in the treeline region

The tree growth-climate relationship indicated that both temperature and precipitation are the main

limiting factor for the growth of *A. spectabilis* in the alpine treeline ecotone in the Mustang region (Figure 5). The tree-ring width chronology showed a significant positive correlation with August precipitation and a positive but non-significant correlation during the spring and summer seasons. In case of temperature, it exhibited predominantly negative correlation, with significant negative relationship with Tmean and Tmax of the previous year September, as well as Tmax of the current year August (Figure 5). However, significant positive correlations were found with Tmax and Tmean of the previous year December and with Tmean in July. Seasonal climatic correlations were relatively weak, but there was a significant positive relationship with winter Tmax, while the summer Tmax showed a significant negative relationship (Figure 5)

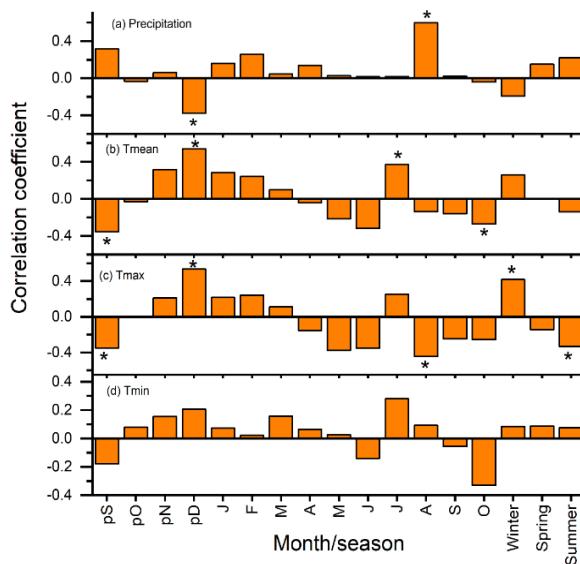


Figure 5 Growth climate response of *Abies spectabilis* in Mustang based on bootstrapped correlation coefficient between the tree-ring chronology and monthly and seasonal climatic data (precipitation and temperature) of Jomsom station. The “*” symbol indicates significant correlation coefficient. A 14-month dendroclimatic window starting from previous year September (pS) until current year October (O) is used.

Temporal stability of growth-climate relationship

Knowing the temporal stability of the growth-climate response is very important for forest management in the context of climate change. Our study found some temporal shifts in the growth limiting factor, though persistent response with the climate data of some months was also found (Figure 6). However, the relationship with Tmean of July, precipitation of January, February, April and May has weakened in recent years (Figure 6). The relationship with July precipitation is becoming more negative during recent years, which could be related to increasing cloud cover during the early monsoon season. The importance of winter precipitation has been weakening during recent years. Moving response with spring month climate is relatively weak and unstable over time (Figure 6).

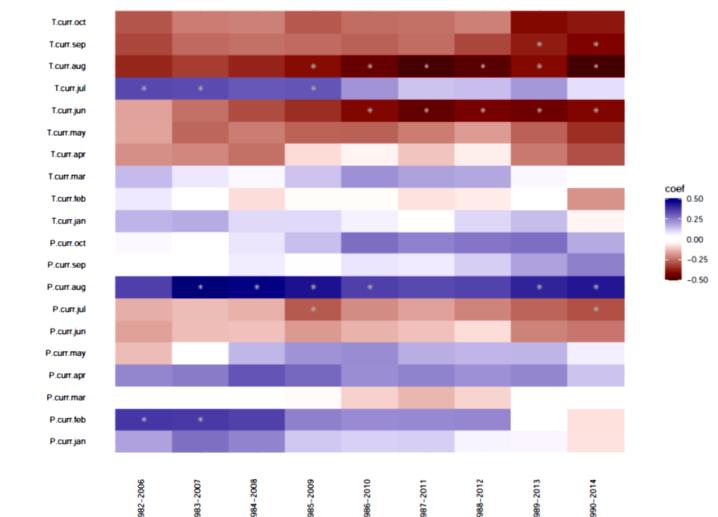


Figure 6 Moving correlation between the tree-ring chronology of *Abies spectabilis* and climate data (T =temperature, P = precipitation) to check temporal stability of growth climate response in Mustang. The “*” symbol indicates statistically significant correlation at 95% or above confidence level

DISCUSSION

Tree growth in alpine treeline ecotone

Nepal Himalayas, including the Mustang region, are experiencing rapid climate change with widespread impacts on natural and socioecological systems (Aryal et al., 2020; Chaudhary et al., 2023; ICIMOD, 2023). In this study, we studied the impact of the climate change on the growth dynamics and climatic sensitivity of the treeline forming *A. spectabilis* in the Mustang region. We developed a century-long tree-ring width chronology of *A. spectabilis* from the treeline ecotone of the ACA, which demonstrated strong dendroclimatic suitability, as indicated by the R-bar and EPS statistics (Briffa, 1995; Wigley et al., 1984). The EPS value exceeded the commonly accepted threshold value of 0.85 (Wigley et al., 1984) from 1949, indicating a representative of population signal. The presence of distinct narrow and wide rings further suggests that *A. spectabilis* in the studied region is highly sensitive to interannual climate variability. The chronology statistics obtained in the study are comparable to those reported in the earlier studies from Mustang and other Himalayan regions (Kharal et al., 2014, 2017; Chhetri & Cairns, 2016; Tiwari et al., 2017a, b; Aryal et al., 2020; Panthi et al., 2020; Gautam et al., 2021). Although the chronology length is relatively short due to the focus on treeline for sampling, much longer *Abies* chronologies (up to ~600 years) have been developed from lower elevations in Nepal (Cook et al., 2003). Average annual radial growth of *A. spectabilis* found in the present study (0.37 mm per year) is lower than the values reported for the same species in other treeline regions, including the Mt Everest region, Manang, Manaslu, Rara and Gaurishankar (Kharal et al., 2017; Tiwari et al., 2017a; Gaire et al., 2020; 2023b; Panthi et al., 2020). The lower growth rate observed in this study likely reflects the cold and dry climate of the

region. Moreover, the variations in growth rates of *A. spectabilis* across sites may be influenced by difference in the tree age and local topo-climatic conditions (Fritts, 1976; Speer, 2010).

The BAI chronology indicated that *A. spectabilis* in the treeline ecotone in Mustang is relatively young and currently in an active growth phase, with an overall positive growth trend. However, the slight decrease in BAI in the recent few years may be associated with the increasing drought condition in the region (Aryal et al., 2017; Gaire et al., 2019). At a global scale, an alpine treeline ecotone is assumed to be formed due to the low temperature limitation during the growing season (Körner, 2012). Thus, in the absence of moisture constraint, warming is often expected to enhance tree growth by alleviating low-temperature limitations (Pandey et al., 2020; Panthi et al., 2020). The BAI chronology of *A. spectabilis* from the treeline ecotone in the Mustang region showed a positive growth trend over time. The increasing trend in BAI is a natural process because the raw BAI chronology generally follows the sigmoid growth curve (Tiwari et al., 2017b; Baral et al., 2022; Gaire et al., 2023b; Klesse & Bigler, 2025). As most sampled trees are less than 100 years old, the increasing BAI could to some extent be the result of the growing stage of the forest. Previous studies of Nepal Himalayas' tree-rings have documented both increasing and decreasing growth trends, depending on site-specific moisture availability (Tiwari et al., 2017b; Panthi et al., 2020; Camarero et al., 2021; Baral et al., 2022; Gaire et al., 2023). The recent decline in BAI found in this study is consistent with the findings on another treeline species, *Betula utilis*, in Mustang, where a slight decrease in BAI of *Betula* at its dry lower limit is reported (Tiwari et al., 2017b). Such coherence in long-term growth trends across species and sites suggests that climate change may be influencing multiple forest species across a broad region (IPCC, 2022).

Growth-climatic relationship in treeline ecotone of Mustang

Plant growth is influenced by a range of biotic and abiotic factors, among which, climatic variables play a dominant role (Fritts, 1976). Depending on site conditions, growth can be limited by temperature, precipitation or their combined effects (ie drought) (Fritts, 1976; Körner, 2012). Our climate-growth relationship analysis shows that radial growth of *A. spectabilis* in the alpine treeline ecotone in the central Himalayas is primarily limited by temperature and secondarily by moisture stress, due to either low precipitation or temperature-induced moisture stress, particularly during the growing season. As the alpine treeline region is the high elevation site with a short growing season, high temperature during the growing season generally enhances photosynthesis and growth (Körner, 2012; Pandey et al., 2020; Gaire et al., 2023b). However, in dry sites, high temperature, accompanied by low precipitation, can suppress growth (Fritts, 1976; Liang et al., 2014; Sigdel et al., 2024; Lu et al., 2025). Our findings indicate that favourable climatic conditions during July–August are very critical for the growth of *A. spectabilis* because this period is the peak growing season in the alpine treeline ecotone of the Himalayas (Körner, 2012). Warm conditions in July and

moist conditions in August were particularly conducive to the growth of *A. spectabilis*. This is because, July typically maintains a positive moisture balance, and elevated temperatures during the month generally promote the growth of *A. spectabilis* in the treeline ecotone in our study area. In contrast, high temperature towards the end of the growing season negatively affect growth, as indicated by the negative relationship and low moisture balance during the period. The trans-Himalayan region receives relatively low annual rainfall, and hence high temperature without sufficient water can negatively affect growth. Some studies have found a positive relationship between growth and temperature during the summer season in the treeline ecotone in the Nepal Himalayas (Chhetri & Cairns, 2016; Gaire et al., 2023b), while some found negative relationship in some dry sites (Cook et al., 2003; Gaire et al., 2019). In some of the Himalayan treelines, precipitation has also emerged as an important controlling climatic driver for tree growth (Liang et al., 2014; Sigdel et al., 2018, 2024). As the present treeline ecotone study site lies in a dry trans-Himalayan mountain slope, with about 300 mm annual rainfall, moisture stress is expected, particularly during the early and later parts of the growing season. The positive correlations observed with early summer precipitation and maximum temperature suggest that warm and wet conditions during summer are beneficial for radial growth (Tiwari et al., 2017b; Pandey et al., 2020; Gaire et al., 2020, 2023b). In the treeline of the Lete area of Mustang (south of the current study), Kharal et al (2014) also found a positive relationship with pre-monsoon precipitation and predominantly negative correlation with temperature, which is consistent with our results. Similarly, in the treeline ecotone near Chimang in Mustang, temperature showed a largely negative influence on growth, whereas precipitation showed a positive effect (Tiwari et al., 2017a). The positive relationship between tree-ring chronology and winter temperature may reflect the chilling requirement of trees in cold climate regions (Luedeling et al., 2011; Guo et al., 2014). A high temperature in winter may promote early snowmelt and improve soil moisture for early season growth (Chhetri & Cairns, 2016; Shah et al., 2019; Gaire et al., 2020, 2023b). A positive relationship with summer minimum temperature but a negative relationship with maximum temperature may indicate the temperature threshold and moisture balance effect on tree growth (Fritts, 1976). Although the direction of the correlation with spring precipitation aligns with previous Himalayan treeline studies, the strength of the relationship in our site is comparatively weak (Liang et al., 2014; Tiwari et al., 2017a,b; Kharal et al., 2017). This may reflect the high elevation aridity of the trans-Himalayan environment, where moisture limitations during the early growing season are particularly pronounced.

Temporal stability of growth-climate response

Understanding the stationarity of growth limiting factor is very crucial for sustainable forest management in the context of climate change. In our study, we found temporally stable to changing response of tree growth with monthly temperature and precipitation data. Relationship with summer month

temperature is negatively intensified, while the positive response to winter month precipitation is becoming weaker. The intensified negative response to temperature could be owing to increasing drought events due to rapid increase in temperature. There are no moving response analysis studies found from the trans-Himalayan region of Nepal for direct comparison of findings; however, studies from southern slopes of the Himalayan mountains have found stable to changing growth-climate response of *A. spectabilis* (Schwab et al., 2018; Gaire et al., 2020, 2023). A study of the treeline in Manaslu did not find a major shift in the growth limiting factor of *Abies* (Gaire et al., 2020); however, in the Gaurishankar region, there is a temporal shift in the growth limiting factor for the same species (Schwab et al., 2018). The diversity in the temporal stability and spatial variability in the growth-limiting climatic factors in different regions of the Nepal Himalayas indicate that climate change may affect tree species in diverse ways (Schwab et al., 2018; IPCC, 2022; Gaire et al., 2020, 2023b). The temporally unstable growth-climate relationships identified in our study highlight the need for dynamic forest management and biodiversity conservation approaches to reduce the vulnerability of treeline species, particularly in the climate-sensitive trans-Himalayan region of Nepal.

CONCLUSION

This study developed a tree-ring width chronology of *A. spectabilis* from the treeline ecotone of the trans-Himalayan region of Mustang, demonstrating its strong potential for dendroclimatic studies. The growth of *A. spectabilis* in the study's treeline site was mainly controlled by temperature and moisture balance during the growing season and preceding to the growing season. We also detected temporal shifts in the growth-limiting factors, indicating that the climatic sensitivity of the species is not stationary. The observed temporal unstable growth-climate response, combined with the recent decline in BAI, suggests that increasing frequency and intensity of drought events under global warming could negatively impact forest growth and treeline dynamics in this region. Therefore, forest managers need to adapt dynamic climate-responsive forest management and conservation strategies to safeguard treeline species in the trans-Himalayan landscape.

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REFERENCES

Adhikari, A.P. & Mathema, A.B. (2023). Examining trends in temperature and precipitation mean/extremes over Gandaki Province, Nepal. *Journal of Water and Climate Change*, 14(7), 2342-2361. doi: 10.2166/wcc.2023.066

Adhikari, S., Timilsina, R.H., Panthee, A.A., & Sapkota, A. (2024). Farmers' perceptions of the impact of climate change on apple production in lower Mustang, Nepal. *Archives of Agriculture and Environmental Science*, 9(1), 8-13, <https://dx.doi.org/10.26832/24566632.2024.090102>

Aryal, P.C., Dhamala, M.K., Gaire, N.P., Bhatta, S., Suwal, M.K., Bhuju, D.R., & Chhetri, P.K., (2020). Tree-ring climate response of two *Larix* species from the central Nepal Himalaya. *Tropical Ecology*, 61, 215–225. <https://doi.org/10.1007/s42965-020-00082-w>

Aryal, S., Ghimire, S.K., Dhakal, Y.R., Gaire, N.P., & Bhandari, S., (2017). Perceptions of agro-pastoralists towards the change in temperature and precipitation in the trans-Himalayan regions of Nepal. *Banko Janakari*, 27 (1), 21–30. <https://doi.org/10.1007/s42965-020-00082-w>

Aryal, S., Grießinger, J., Dyola, N., Gaire, N.P., Bhattarai, T., & Bräuning, A. (2023). INTRAGRO: A machine learning approach to predict future growth of trees under climate change. *Ecology and Evolution*, 13(10), e10626. <https://doi.org/10.1002/ece3.10626>

Bhadra, R., Neupane, B., & Khadka, U.R. (2021). Induced Impacts of Climate Change on Livelihood and Migration in Upper Himalayas: A Case of Mustang, Nepal. *Handbook of Climate Change Management*, 2229-2269. https://doi.org/10.1007/978-3-030-22759-3_303-2

Briffa, K.R. (1995). Interpreting high-resolution proxy climate data the example of dendroclimatology. In: von Storch, H., & Navarra, A. (eds) *Analysis of climate data variability, applications of statistical techniques*, New York, Springer, 77–94.

Bunn, A.G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, 26(2), 115-124. <https://doi.org/10.1016/j.dendro.2008.01.002>

Brunello, C.F., Andermann, C., Helle, G., Comiti, F., Tonon, G., Tiwari, A., & Hovius, N. (2019). Hydroclimatic seasonality recorded by tree ring $\delta^{18}\text{O}$ signature across a Himalayan altitudinal transect. *Earth and Planetary Science Letters*, 518, 148–159. <https://doi.org/10.1016/j.epsl.2019.04.030>

Camarero, J.J., Gazol, A., Sánchez-Salguero, R., Fajardo, A., McIntire, E.J.B., Gutierrez, E., Batllori, E., Boudreau, S., Carrer, M., Diez, J., Dufour-Tremblay, G., Gaire, N.P., Hofgaard, A., Jomelli, V., Kirdyanov, A.V., L'evèque, E., Liang, E., Linares, J.C., Mathisen, I.E., Moiseev, P.A., Sangüesa-Barreda, G., Shrestha, K.B., Toivonen, J.M., Tutubalina, O.V., & Wilmking, M. (2021). Global fading of the temperature-growth coupling at alpine and polar treelines. *Global Change Biology*, 27, 1879–1889. <https://doi.org/10.1111/gcb.15530>

Chhetri, P.K., & Cairns, D.M. (2016). Dendroclimatic response of *Abies spectabilis* at treeline ecotone of Barun Valley, eastern Nepal Himalaya. *J. For. Res.*,

27 (5), 1163–1170. <https://doi.org/10.1007/s11676-016-0249-7>.

Chaudhary, S., Chettri, N., Adhikari, B., Dan, Z., Gaire, N.P., Shrestha, F., & Wang, L. (2023). Effects of a changing cryosphere on biodiversity and ecosystem services, and response options in the Hindu Kush Himalaya, in: *ICIMOD, Water, ice, society, and ecosystems in the Hindu Kush Himalaya: An outlook*, edited by: Wester, P., Chaudhary, S., Chettri, N., Jackson, M., Maharjan, A., Nepal, S., and Steiner, J.F., ICIMOD, 123–163. <https://doi.org/10.53055/ICIMOD.1032>

Cook, E.R., & Kairiukstis, L.A. (1990). *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, the Netherlands. 414 pp.

Cook, E.R., Krusic, P.J., & Jones, P.D. (2003). Dendroclimatic signals in long tree-ring chronologies from the Himalayas of Nepal. *International Journal of Climatology*, 23 (7), 707–732. <https://doi.org/10.1002/joc.911>

Dawadi, B., Liang, E., Tian, L., Devkota, L.P., & Yao, T. (2013). Pre-monsoon precipitation signal in tree rings of timberline *Betula utilis* in the central Himalayas. *Quaternary International*, 283, 72–77. <https://doi.org/10.1016/j.quaint.2012.05.039>

DHM, (2017). *Study of climate and climatic variation over Nepal*. Department of Hydrology and Meteorology, Ministry of Science, Technology and Environment, Government of Nepal, Kathmandu, Nepal

DNPWC, (2019). *Protected areas of Nepal*. Department of National Parks and Wildlife Conservation, Kathmandu, Nepal.

Fort, M. (2014). Natural hazards versus climate change and their potential impacts in the dry, northern Himalayas: focus on the upper Kali Gandaki (Mustang District, Nepal). *Environmental Earth Sciences*, 73 (2), 801–814. <https://doi.org/10.1007/S12665-014-3087-Y>

Fort, M., Gurung, N., Arnaud-Fassetta, G., & Bell, R. (2024). Retrospect of the polygenetic Kagbeni flood event (August 13, 2023) in Mustang, Nepal. Are rapid hydro morphological processes relays and sediment cascades in the catchment well taken into account in the risk equation?, EGU General Assembly 2024, Vienna, Austria, 14–19 Apr 2024, EGU24-2563, <https://doi.org/10.5194/egusphere-egu24-2563, 2024>.

Fritts, H.C. (1976). *Tree Rings and Climate*. Cambridge University Press, Cambridge, 567 pp.

Gaire, N.P., Fan, Z.-X., Chhetri, P. K., Shah, S. K., Bhuju, D. R., Wang, J., Sharma, B., Shi, P., & Dhakal, Y.R. (2023a). Treeline Dynamics in Nepal Himalaya in a Response to Complexity of Factors. In: S.P. Singh, Z.A. Reshi, & R. Joshi (eds.), *Ecology of Himalayan Treeline Ecotone*, Springer, pp. 519–563.

Gaire, N. P., Zaw, Z., Bräuning, A., Grießinger, J., Sharma, B., Rana, P., Bhandari S., Basnet, S., & Fan, Z.X. (2023b). The impact of warming climate on Himalayan silver fir growth along an elevation gradient in the Mt. Everest region, *Agricultural and Forest Meteorology*, 339, 109575.

Gaire, N.P., Fan, Z.X., Bräuning, A., Panthi, S., Rana, P., Shrestha, A., & Bhuju, D.R. (2020). *Abies spectabilis* shows stable growth relations to temperature, but changing response to moisture conditions along an elevation gradient in the central Himalaya. *Dendrochronologia*, 60, 125675.

Gaire, N.P., Dhakal, Y.R., Shah, S.K., Fan, Z.X., Brauning, A., Thapa, U.K., Bhandari, S., Aryal, S., & Bhuju, D.R. (2019). Drought (scPDSI) reconstruction of trans-Himalayan region of central Himalaya using *Pinus wallichiana* tree-rings. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 514, 251–264. <https://doi.org/10.1016/j.palaeo.2018.10.026>.

Gautam, D., Shrestha, N.M., Gaire, N.P., Roth, B.E., Jandug, C.M.B., Tong, X.J., & Liu, Q.J. (2021). A 99-year chronology of blue pine (*Pinus wallichiana*) tree-rings concerning interannual climate variability in the central Himalayas of Nepal. *Appl. Ecol. Environ. Res.*, 19, 3519–3532.

Ghimire, N.P., Ghimire, P., Chauhan, R., & Thakuri, S. (2025). Climatic Trends and Their Impacts on High-Altitude Ecosystems in Nepal: Implications for Biodiversity and Ecosystem Services. *Journal of Environment Sciences* (2025), 11, 63–76. <https://doi.org/10.3126/jes.v11i1.80589>

Gmińska-Nowak, B. & Ważny, T. (2020). Dendrochronological analysis of the ancient architecture of Kingdom of Lo. Upper Mustang, Nepal. *Dendrochronologia*, 61, 125701. <https://doi.org/10.1016/j.dendro.2020.125701>

Guo, L., Dai, J., Ranjitkar, S., Yu, H., Xu, J., & Luedeling, E. (2014). Chilling and heat requirements for flowering in temperate fruit trees. *Int. J. Biometeorol.*, 58 (6), 1195–1206. <https://doi.org/10.1007/s00484-013-0714-3>

Hamal, R., Thakuri, B.M., Poudel, K.R., Gurung, A., & Yun, S.J. (2022). Farmers' perceptions of climate change in Lower Mustang, Nepal. *Environ Monit Assess.*, 194(9), 606. doi: 10.1007/s10661-022-10286-3. PMID: 35867162

Harris, I., Osborn, T.J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, 7 (1), 1–18. <https://doi.org/10.1038/s41597-020-0453-3>

Holmes, R.L. (1983). Computer assisted quality control in tree ring dating and measuring. *Tree-Ring Bulletin*, 43, 69–78.

ICIMOD, (2023). *Water, ice, society, and ecosystems in the Hindu Kush Himalaya: An outlook*, edited by: Wester, P., Chaudhary, S., Chettri, N., Jackson, M., Maharjan, A., Nepal, S., and Steiner, J. F., ICIMOD, Lalitpur, Nepal.

DOI:10.53055/ICIMOD.1028

IPCC, (2022). *Climate change 2022: Impacts, adaptation, and vulnerability*. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change [Pörtner, H.O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegria, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., & Rama, B. (Eds.)]. Cambridge University Press, Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 3056.

Karki, R., ul Hasson, S., Schickhoff, U., Scholten, T. & Böhner, J. (2017). Rising precipitation extremes across Nepal. *Climate*, 5 (1), 4. <https://doi.org/10.3390/CLJ5010004>.

Kharal, D.K., Meilby, H., Rayamajhi, S., Bhuju, D., & Thapa, U.K. (2014). Tree ring variability and climate response

of *Abies spectabilis* along an elevation gradient in Mustang, Nepal. *Banko Janakari*, 24, 3–13.

Kharal, D.K., Thapa, U.K., St. George, S., Meilby, H., Rayamajhi, S., & Bhuju, D.R. (2017). Tree-climate relations along an elevational transect in Manang Valley, central Nepal. *Dendrochronologia*, 41, 57–64. <https://doi.org/10.1016/j.dendro.2016.04.004>.

Körner, C. (2012). *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer.

Klesse, S., & Bigler, C. (2025). Growth trends in basal area increments: The underlying problem, consequences for research and best practices. *Dendrochronologia*, 90, 126296. <https://doi.org/10.1016/j.dendro.2025.126296>

Liang, E.Y., Dawadi, B., Pederson, N., & Eckstein, D. (2014). Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology*, 95, 2453–2465. <https://doi.org/10.1890/13-1904.1>

Lu, X., Zheng, X., Liang, E. et al. (2025). Patterns, dynamics and drivers of alpine treelines and shrublines. *Nat Rev Earth Environ*, 6, 489–502 (2025). <https://doi.org/10.1038/s43017-025-00703-9>

Luedeling, E., Girvetz, E.H., Semenov, M.A., & Brown, P.H., (2011). Climate change affects winter chill for temperate fruit and nut trees. *PLoS One*, 6 (5), e20155. <https://doi.org/10.1371/journal.pone.0020155>

Meier, W.J.H., Pohle, P., & Grießinger, J. (2022). Climate Change and New Markets: Multi-Factorial Drivers of Recent Land-Use Change in The Semi-Arid Trans-Himalaya, Nepal. *Land* 11, 1567. <https://doi.org/10.3390/land11091567>

Melvin, T.M., & Briffa, K.R. (2008). A signal-free approach to dendroclimatic standardization. *Dendrochronologia* 26 (2), 71–86.

MoFE, (2021a). *Vulnerability and Risk Assessment and Identifying Adaptation Options: Summary for Policy Makers*. Ministry of Forests and Environment, Government of Nepal. Kathmandu, Nepal.

MoFE, (2021b). *Vulnerability and Risk Assessment and Identifying Adaptation Options in the Forest, Biodiversity and Watershed Management in Nepal*. Ministry of Forests and Environment, Government of Nepal. Kathmandu, Nepal

Pages 2k Consortium, (2013). Continental-scale temperature variability during the past two millennia. *Nature. Geosci.*, 6, 339–346. <https://doi.org/10.1038/ngeo1797>

Pandey, S., Cherubini, P., Saurer, M., Carrer, M., & Petit, G. (2020). Effects of climate change on treeline trees in Sagarmatha (Mt. Everest, Central Himalaya). *Journal of Vegetation Science*, 31 (6), 1144–1153.

Panthi, S., Fan, Z.X., van der Sleen, P., & Zuidema, P.A. (2020). Long-term physiological and growth responses of Himalayan fir to environmental change are mediated by mean climate. *Global Change Biology*, 26, 1778–1794. <https://doi.org/10.1111/gcb.14910>

Poudel, D.D., & Duex, T.W. (2017). Vanishing springs in Nepalese mountains: Assessment of water sources, farmers' perceptions, and climate change adaptation. *Mountain Research and Development*, 37(1), 35–46.

Rinn, F. (2003). *TSAP-Win: time series analysis and presentation for dendrochronology and related applications*. Version 0.55 User reference. Heidelberg, Germany. Available at: <http://www.rimatech.comSalzer>

Schmidt, B. (1992-93). Dendrochronological Research in Southern Mustang Mustang. *Ancient Nepal*, 130-133:20-33.

Schmidt, B., Wazny, T., Malla, K., Höfs, E. & Khalessi, M. (1999). Chronologies for historical dating in high Asia/Nepal. In: R. Wimmer and R.E. Vetter, eds., *Tree-Ring Analysis: Biological, Methodological, and Environmental Aspects*. CABI Publishing, Oxon, United Kingdom, 205-211.

Sherchan, P. (2019). Understanding the Nexus of Climate Change and Migration: A Case of Dhye Peoples from Upper Mustang, Nepal. *Grassroots Journal of Natural Resources*, 2(1-2): 1-19. <https://doi.org/10.33002/nr2581.6853.02121>

Shah, S.K., Pandey, U., Mehrotra, N., Wiles, G.C., & Chandra, R. (2019). A winter temperature reconstruction for the Lidder Valley, Kashmir, Northwest Himalaya based on tree-rings of *Pinus wallichiana*. *Climate Dynamics*, 53(7–8), 4059–4075. <https://doi.org/10.1007/s00382-019-04773-6>

Sigdel, K.P., Ghimire, N.P., Pandeya, B. & Dawadi, B. (2022). Historical and projected variations of precipitation and temperature and their extremes in relation to climatic indices over the Gandaki River Basin, Central Himalaya. *Atmosphere*, 13 (11), 1866. <https://doi.org/10.3390/ATMOS13111866>

Sigdel, S.R., Wang, Y., Camarero, J.J., Zhu, H., Liang, E., & Peñuelas, J. (2018). Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. *Global Change Biology*, 24(11), 5549–5559. <https://doi.org/10.1111/gcb.14428>

Sigdel, S.R., Zheng, X., Babst, F. et al. (2024). Accelerated succession in Himalayan alpine treelines under climatic warming. *Nature. Plants*, 10, 1909–1918 (2024). <https://doi.org/10.1038/s41477-024-01855-0>

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

Tiwari, A., Fan, Z.X., Jump, A.S., Li, S.F., & Zhou, Z.K. (2017a). Gradual expansion of moisture sensitive *Abies spectabilis* forest in the Trans-Himalayan zone of central Nepal associated with climate change. *Dendrochronologia*, 41, 34–43. <http://dx.doi.org/10.1016/j.dendro.2016.01.006>

Tiwari, A., Fan, Z.-X., Jump, A.S., & Zhou, Z.K. (2017b). Warming induced growth decline of Himalayan birch at its lower range edge in a semi-arid region of Trans-Himalaya, central Nepal. *Plant Ecology*, 218 (5), 621–633. <https://doi.org/10.1007/s11258-017-0716-z>

Wigley, T.M.L., Briffa, K.R., & Jones, P.D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23, 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023<0201:OTAVOC>2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2)

Zang, C., & Biondi, F. (2015). Treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38(4), 431–436. <https://doi.org/10.1111/ecog.01335>