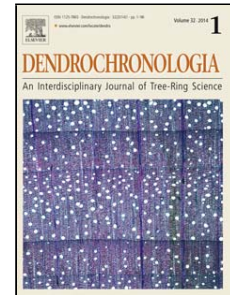# Accepted Manuscript

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Growth variable-specific moisture and temperature limitations in co-occurring alpine tree and shrub species, central Himalayas, Nepal

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Abstract

Trees and shrubs found in the forest-tundra ecotone (FTE) are considered to be highly sensitive to climate change, but their response to climatic drivers is only partially understood. We use dendrochronological techniques to develop growth chronologies for co-occurring tree (*Abies spectabilis*, radial growth and height) and dwarf shrub (*Cassiope fastigiata*, stem elongation and leaf number) species in central Himalaya, Nepal, in order to identify and compare climate drivers of growth (temperature, precipitation, moisture (SPEI)). Our results reveal growth variable-specific responses characterized by a predominant response to previous year and non-growing season climate, and to length of the monsoon season. Tree radial growth was significantly correlated with temperature during previous summer and non-growing season months, and moisture in the late monsoon (September). Tree height increment correlated with late-monsoon temperature and moisture in the previous post-monsoon. Shrub stem elongation mainly correlated with temperature and moisture conditions in previous-year pre-monsoon (May), while leaf production correlated with moisture in previous pre-monsoon and monsoon periods, and precipitation in the late-monsoon. These results contribute new evidence that mid-latitude FTE tree and shrub species and individual growth variables are limited by unique climate drivers operational at different periods during and outside the monsoon season. Within the context of rising temperatures and increased precipitation variability in the Himalayas, moisture may become a more frequent stressor on tree and shrub growth. Consideration of climate and site variable interactions at alpine sites is important to detecting subtleties of growth response. Dendroecological studies of co-occurring tree and shrub species help to identify concomitant and disparate growth responses to climate drivers and in turn, provide information and insight into FTE changes in the Himalayas and elsewhere.
Key words: *Abies spectabilis, Cassiope fastigiata*, dendroecology, forest-tundra ecotone, Himalayas

1. Introduction

High elevation mountains are sensitive to climate change (Rangwala and Miller, 2012) and recent evidence suggests elevation-dependent warming in mountain regions on a global scale (Mountain Research Initiative EDW Working Group, 2015). In the Nepal Himalayas, recent studies indicate changing climatological conditions over the past several decades including rising

temperatures (Shrestha et al., 1999; Kattel and Yao, 2013; Shrestha et al., 2012; Salerno et al., 2015), variable precipitation patterns (Shrestha et al., 1999; Xu et al., 2009; Yao et al., 2012; Shrestha et al., 2012; Salerno et al., 2015) and a weakening Indian monsoon (Wu et al., 2003; Thompson et al., 2006; Wang and Ding, 2006; Zhou et al., 2008). The effect of these climatic changes upon the vegetation is not well quantified, including understanding of primary drivers, synergistic interactions with other environmental variables, feedbacks with the atmosphere and hydrosphere, and related effects on ecosystem services.

Trees and shrubs found at the forest-tundra ecotone (hereafter FTE) are considered to be highly sensitive to climate change (Tranquillini et al., 1979; Körner and Paulsen, 2004; Hofgaard et al., 2009; Hallinger et al., 2010) and thus, understanding their response to a changing climatological context in the Himalayas has been the subject of recent research (Gaire et al., 2014; Schickhoff et al., 2015; Shrestha et al., 2015; Chhetri and Cairns, 2016; Suwal et al., 2016; Bhuju, 2016). In the last decade, the number of dendroclimatological and dendroecological studies of tree species found in the Himalayas and the Tibetan Plateau has increased (Cook et al., 2003; Sano et al., 2005; Cook et al., 2010; Liang et al., 2014). Research on alpine shrubs in the Himalayas and elsewhere also continues to expand (Bär et al., 2008; Hallinger, 2010; Myers-Smith et al., 2011; Rayback et al., 2012a; Liang et al., 2012; Li et al., 2013; Myers-Smith et al., 2015), extending the reach of dendrochronological techniques into tree-less environments and initiating the beginning of a spatially-continuous network of proxies across vegetation communities. Understanding the response of co-occurring tree and shrub species to climate, now and in the future, may help to elucidate the physiological mechanisms controlling local and landscape-scale transitions from forest to shrub tundra.

Research on trees and shrubs in the Himalayas and Tibetan Plateau has yielded heterogeneous results in terms of climate drivers. In some cases, and in line with ecological theory (Körner and Paulsen, 2004; Wieser and Tausz, 2007), temperature is considered the primary limitation on growth (Yadav and Bhattacharyya, 1992; Bräuning et al., 2004; Li et al., 2013). Alternatively, evidence from other studies points to moisture availability as the limiting factor (Singh et al., 2006; Sano et al., 2010; Borgaonkar et al., 2011; Dawadi et al., 2013; Yang et al., 2013; Liang et al., 2014). Of these studies, none examined the climate drivers of growth of tree and shrub species co-occurring in the FTE.

The objectives of this study were twofold: first, develop growth chronologies for two co-occurring but functionally different woody species, *Abies spectabilis* (two chronologies: annual tree-ring widths and annual height-growth) and *Cassiope fastigiata* (two chronologies: annual stem elongation and number of leaves produced per year) at a high elevation FTE site in the central Himalayas, Nepal, and second, identify and compare the climate drivers of growth in these two species. Based on previous research, we hypothesized that *A. spectabilis* growth would respond to a moisture deficit signal in the pre-monsoon season in the year of growth (Sano et al., 2010) and *C. fastigiata* to a late winter-early spring temperature signal (Liang et al., 2015).

2. Material and methods

2.1. Study site

The study area is located on a mesic, north-facing slope of Langtang Valley (28°05'50" N, 85°23'30" E) in the Rasuwa district in the central Himalayas, Nepal (Fig. 1). The valley is situated in the southernmost range of the greater Himalayas with the landscape dominated by rock-fall sediments and glacio-fluvial moraine deposits (Heuberger et al., 1984).

Continental and maritime factors influence the climate of Nepal with the central portion of the Himalayas dominated by the southeast monsoon and orographic effects (Putkonen, 2004; Barr, 2008). The mean annual (pre- and monsoon season (MJJAS)) temperature (1900-2008; CRU TS3.23; Harris et al., 2014) is approximately 3.5°C (9.7°C) (Fig. 2). The approximate mean temperature of the warmest month (July) is 11.3°C, and the coldest (January) is -5.4°C. In the central Himalayas, temperatures rise rapidly in May and June and then quickly decrease in September. Monsoonal precipitation (1900-2008; CRU TS3.23; Harris et al., 2014) between June and September (~771 mm) accounts for approximately 71% of total annual precipitation (~1087 mm) at this site, while snowpack (~21% of annual total) is present from November to March (Fig. 2). Monsoonal precipitation typically lags behind temperature, peaking in July and August. Precipitation in the central Himalayas is altitude-dependent (Putkonen, 2004; Ichiyanagi et al., 2007; Barr, 2008). Measurements by the Tropical Rainfall Measuring Mission (TRMM) satellite show an increase in annual precipitation from the lowlands to 2000 m.a.s.l., then a decline with increasing elevation and latitude (http://disc.sci.gsfc.nasa.gov/daac-bin/tcc.pl; Liang et al., 2014). Precipitation totals are strongly influenced by smaller scale wind patterns, as well as slope aspect

(Barr, 2008). Variations in topography over small scales may also influence local climate conditions.

Recent analysis has shown that surface temperatures have increased across the Himalayas by 1.5°C from 1982-2006 (0.06°C yr^{-1}) and that overall, average precipitation has increased, but with notable seasonal, annual, and geographic variability (Shrestha et al., 2012). There have been significant increases in annual and seasonal temperatures, increases in annual, spring and summer precipitation and declines in fall and winter precipitation in ecoregions in and around the study site (Shrestha et al., 2012).

Evidence of grazing, trampling, logging and burning was apparent in the region, and as the FTE is actively utilized by pastoralists, it was not possible to find sampling sites completely devoid of recent human activity.

2.2. Abies spectabilis and Cassiope fastigiata

One tree and one shrub species in close spatial proximity were investigated in this study. Distributed from East Nepal to eastern Afghanistan, *Abies spectabilis* (D. Don) Spach (Himalayan silver fir) typically occurs on the southern flank of the Himalayas, forming forests at higher elevations (~2,700 to 4,000 m.a.s.l.). It is a dominant forest species (mean height: 24-40 m) in the central and western regions of Nepal, but may also occur as stunted individuals at higher elevations (Ghimire and Lekhak, 2007). It is associated with other conifer and broadleaf trees and shrubs on southern (e.g., *Quercus semecarpifolia*) and northern (*Quercus* spp, *Rhododendron campanulatum*, *R. lepidotum*, and *R. anthopogon*) slopes (Ghimire and Lekhak, 2007), as well as *Betula utilis* and *Salix* spp. on more arid sites (Liang et al., 2014). The species grows best on moist and shady, north-facing slopes, preferring acidic and clay soils.

The shrub species, *Cassiope fastigiata* (Wall.) D. Don (Himalayan heather), is an evergreen, dwarf shrub (*Ericaceae*) found on both north- and south-facing slopes and distributed across an altitudinal range of 2,800 to 4,500 m.a.s.l. in the southern Himalayas in Nepal, Bhutan, India and Pakistan, as well as in Yunnan, China and Tibet (Polunin and Stainton, 1984). *C. fastigiata* thrives in the more open portion of the FTE with *Rhododendron* species as dominant components and the sparse occurrence of *A. spectabilis* seedlings and saplings. Shrubs may attain a height of 30 cm and are characterized by a decumbent form and stiff, multi-branched stems (Polunin and Stainton, 1984). Plant propagation via layering occurs in *C. fastigiata*,

resulting in multiple short stems. The shrub's leaves are ovate (4–6 mm long and 1.5–2 mm wide) with a deep furrow and hyaline margin. As characteristic of the genus *Cassiope*, two alternating sets of opposite leaves form four distinct rows along the stem. Smaller leaves formed in the early and late growing season, bracket larger leaves formed during the summer. This wave-like pattern in leaf lengths was first described by Warming (1908) for the circumpolar heather, *Cassiope tetragona* (L.) D. Don. Callaghan et al. (1989) used the leaf pattern to identify and date individual years of growth for *C. tetragona* and develop chronologies of annual growth. Later, Johnstone and Henry (1997) discovered leaf node scar patterns in adjacent leaf rows were analogous to the wave-like pattern in leaf-lengths and, as leaf scars are visible along the stem for long periods of time, they can be used to develop longer chronologies of annual growth and reproduction (Rayback and Henry, 2006). This technique has also been used to identify and date annual growth in the North American shrub, *C. mertensiana* (Bong) D. Don (Rayback, 2012a).

2.3. Field sampling

Abies spectabilis trees and saplings were sampled between the elevations of 3750 and 3960 m.a.s.l. in June 2008 (trees: up to 3910 m a.s.l.). The sampling area encompassed a 100 m wide band perpendicular to the slope covering two kilometers horizontal distance. Location coordinates and the elevation of each sampled tree, sapling and shrub individual were recorded using GPS. Xylem increment cores were collected from mature, dominant trees. Two cores per tree (n=24 trees) were extracted at a height of 50-80 cm above ground surface with a 5 mm increment borer at 180° to each other and perpendicular to the dominant slope. Sixty *A. spectabilis* saplings (height: 50-199 cm) were sampled for annual height growth. The annual height growth measurements of young individuals were identified by clearly visible branch nodes along the stem length and were recorded with a ruler to the nearest 0.5 cm (Shrestha et al., 2014).

Cassiope fastigiata plants were collected between the elevations of 3750 and 3960 m. a.s.l. in June and July 2008. Twenty-seven green-tipped and flowering individuals of *C. fastigiata* were harvested. Sampled plants were spaced at least 100 m apart to ensure each individual was genetically distinct. The entire plant, including roots, was removed from the site, air dried and stored in paper bags. As an objective of this study was to compare the climatic

drivers of growth in co-occurring *C. fastigiata* and *A. spectabilis* in the FTE, *C. fastigiata* plants were selected for their potential to cover the time span of *A. spectabilis* height growth.

2.4. Chronology construction

Abies spectabilis xylem cores were processed according to standard dendrochronological techniques (Stokes and Smiley, 1996). Tree-ring widths were measured using an electronic analysis bench (LINTAB: TSAP, Heidelberg, Germany) and a binocular microscope to an accuracy of 0.01 mm. The tree-ring width (hereafter TRW) and the annual height-growth (hereafter height growth increment; HGI) series were visually crossdated and verified statistically using COFECHA (Holmes, 1983). Individual series were removed from the master chronologies if COFECHA-identified dating errors could not be resolved.

Two to four dominant *C. fastigiata* stems were analyzed from each of the plants sampled. Distances between leaf internode scars were measured under a microscope connected to a Velmex unislide traversing table, an Accu-rite encoder (0.001 mm) and a Quick-Chek digital readout system. Individual stem measurement series were processed and plotted in a spreadsheet program for visual crossdating. Annual stem elongation (hereafter annual growth increment; AGI) were identified by wave-like patterns in internode lengths, with the terminus of each year of growth marked by the shortest internode length at the end of each wave-series (Johnstone and Henry 1997) (Fig. 3). Due to the short stem lengths (2-7 years), crossdating with COFECHA was not feasible and thus, the site chronology was constructed using meticulous visual crossdating and pointer years (Schweingruber et al., 1990). Individual stems were removed from the site chronology when within- and between-plant correlations, respectively, fell below r = 0.60. Infrequently, short periods of temporarily-arrested growth in stem elongation were identified (Fig. 3), most likely due to unfavorable environmental conditions at the site. The annual production of leaves chronology (hereafter LEAF) was developed by counting the total number of leaves produced each year and crossdating was based on the AGI master chronology. As plants were sampled in June 2008 and stem tips had not fully elongated, all stem chronologies end with the 2007 growth year. Wintermarksepta, a morphological characteristic consisting of dark, dense tissue formed at the end of summer growth when the pith narrows and used to identify annual growth in *C. tetragona* (Rozema et al., 2009) were not visible in *C. fastigiata*.

For a complete description of the chronology construction process, see Rayback and Henry (2005).

Both *A. spectabilis* and *C. fastigiata* time series were standardized in ARSTAN to remove age-related growth trends (Cook, 1985). Standardization results in a time series of dimensionless index values by dividing the observed value by the expected as given by the spline function (Fritts, 1976). The *A. spectabilis* TRW and HGI chronologies were standardized with a negative exponential curve (Table S1). A 32-year cubic spline was fitted to the *C. fastigiata* AGI and LEAF series. The detrended series were prewhitened by removing autocorrelation from each series by using an autoregressive moving average time-series model to produce a residual chronology. The measured values (TRW, HGI, AGI, LEAF) were divided by the fitted regression function to produce dimensionless index series. To further enhance the climate signal, index values from each individual series were averaged using the bi-weight robust mean. Standard and residual chronologies were produced and examined.

For all chronologies, measures of mean sensitivity, interseries correlation, and first-order autocorrelation were calculated to assess chronology quality (Fritts, 1976). Mean sensitivity expresses the year-to-year variability within a series, interseries correlation is the mean correlation calculated among all series, and first-order autocorrelation refers to the correlation of members in a time series at time t with values in the same time series at time, t-1. (Briffa and Jones, 1990). Chronology quality was further examined using the Signal-to-Noise Ratio, the Expressed Population Signal (EPS) and subsample signal strength (SSS) (Wigley et al., 1984). The EPS is a measure of the common variability in a chronology that is dependent upon the sample depth. The recommended threshold for the EPS value is 0.85 (Wigley et al., 1984). SSS is a measure of the amount of signal captured by a subsample of cores from some master chronology (Speer, 2012).

2.5. Climate data

The limited number of meteorological stations, their predominant locations at lower elevations and short climate records riddled with data gaps is problematic for dendrochronological studies in the Himalayas (Cook et al., 2003). The closest meteorological stations to our field site were Dhunche (1982 m a.s.l., 1971-2007) and Kathmandu (1336 m a.s.l., 1968/71-2007), Nepal, both of which were characterized by missing data and site elevations

1788 and 2600 m lower, respectively, than the study site. Therefore, gridded monthly climate data (temperature and precipitation) from University of East Anglia's Climate Research Unit (CRU) (TS3.23 at 0.5° spatial resolution; 26.0 to 32°N, 78.0 to 90°E; Harris et al., 2014) were used. Pearson's correlations comparing the Kathmandu meteorological station and CRU monthly (January, July) and annual temperature data (1968-2007) were significant (P<0.01). Correlations between the two datasets were also significant (P<0.01) for January total precipitation, but not for annual or July total precipitation (P>0.05). The Standardized Precipitation-Evapotranspiration Index (SPEI; http://sac.csic.es/spei/index.html; Vicente-Serrano et al., 2010) was also investigated to understand species' integrated response to moisture availability (i.e., the standardized difference between precipitation and potential evapotranspiration over a given period). The SPEIbase v.2.4 dataset, based on the FAO-56 Penman-Monteith estimate of potential evapotranspiration (Allen et al., 1998), was used in the analyses. The SPEI quantifies drought severity based on its intensity and duration and can delimit the onset and end of drought episodes.

2.6. Statistical analysis

The relationship between the *A. spectabilis* TRW (1946-2007; 1993-2007) and HGI (1993-2007) and the *C. fastigiata* AGI and LEAF chronologies (1999-2007) and climate data derived from CRU TS3.23 (Harris et al., 2014) were initially examined using Pearson's product moment (r) (TRW; 1946-2007) or Spearman's Rank (ρ) (TRW (1993-2007); HGI; AGI; LEAF) correlation coefficients. The original *A. spectabilis* TRW chronology (TRW; 1946-2007) was investigated to assess longer term chronology-climate relationships. The truncated TRW chronology (TRW; 1993-2007) was developed to assess specifically the chronology-climate relationships over a time period common to *both* the TRW and HGI chronologies (1993-2007). The common period of analysis for the *C. fastigiata* AGI and LEAF chronologies was 1999-2007. All correlations were calculated based on overlapping data periods between the chronologies and climate variables for an 18-month window beginning in May of the previous year (*p*) to October of the current year. The period covers the last month of the previous pre-monsoon (May), the monsoon (JJAS) and the post-monsoon (ONDJF) seasons when climatically-induced physiological preconditioning may occur (Fritts, 1976), as well as the current pre-monsoon (MAM), the monsoon (JJAS) and the first month of the post-monsoon

(October) seasons. Monthly climate variables explored included: mean minimum, mean maximum and mean monthly temperature (°C), total monthly precipitation (mm) and the monthly SPEI calculated on a 1-, 3-, 4-, 6- and 12-month basis. Correlations between the growth chronologies and tested climate variables that were not significant ($P>0.05$) were not considered further. Statistical analyses were performed in IBM SPSS Statistics 24 (2016).

Following initial identification of significant ($P<0.05$) climate-chronology relationships, correlation and response functions were run using DENDROCLIM2002 (Biondi and Waikul, 2004). DENDROCLIM2002 employs bootstrapped confidence intervals to compute the significance of correlation and response function coefficients at the $P<0.05$ level. Due to the short length of most of the chronologies, moving window correlations were only carried out on the longer *A. spectabilis* TRW (1946-2007) chronology-climate relationships. A moving interval with the base length of 25-years, moving forward one year at a time, was selected. This produced a series of correlation coefficients that display the development of the climate-growth relationship over time (Wilmking and Myers-Smith, 2008). Both Gleichläufigkeit scores (Schweingruber, 1988) and sign tests (Fritts, 1976) were calculated to assess the similarity between significantly ($P<0.05$) correlated chronologies and climate time series.

3. Results

3.1. Chronology characteristics

To maintain consistency of analysis within species, all *A. spectabilis* chronologies were standardized using the negative exponential spline despite the fact that individual chronology quality statistics may have been stronger using other standardizations (Table S1, Fig. S1a, b, Fig. S2). The *A. spectabilis* TRW and the HGI chronologies are characterized by moderate inter-series correlation values (Table 1). The TRW chronology has a moderate mean sensitivity and a high first-order autocorrelation value while the HGI chronology has opposite characteristics. The EPS values for the longer (1946-2007) and shorter (1993-2007) TRW chronologies were 0.85 (14 trees) and 0.85 (21 trees), respectively (Table S1). For the HGI chronology, the EPS was 0.77 (29 saplings). Despite the fact that the EPS value for the HGI chronology was lower than the recommended threshold (0.85) and that the sample depth for the longer TRW dropped below the required 14 trees prior to 1988 (Table S1; Fig. S2), we used the entire length of the available chronologies for analysis. While the recommended EPS cut off value is typically employed in

climate reconstruction studies, valuable ecological information may be lost if chronologies are truncated using this metric.

The *C. fastigiata* AGI (1999-2007) and LEAF (1999-2007) chronologies were standardized using the 32-year cubic spline to maintain consistency (Table S1). These chronologies are characterized by moderate series intercorrelation and mean sensitivity and low first-order autocorrelation values (Table 1, Fig. S1c, d). While the EPS values for the AGI (0.71, 17 shrubs) and LEAF (0.75, 16 shrubs) chronologies (Table S1) were also below the suggested threshold used in climate reconstructions, the full length of both chronologies were maintained for the analysis.

3.2. Relationships between climate and growth chronologies

Overall, the exploratory climate-growth correlation analyses revealed the significant (P<0.05-0.01) and predominant influence of the previous pre-monsoon, monsoon and post-monsoon season climate on both *A. spectabilis* and *C. fastigiata* growth. For *A. spectabilis* TRW (1993-2007), correlation analyses identified significant (P<0.05-0.01) and positive relationships with temperature (T_{min}, T_{max} and T_{mean}) for multiple individual months between p June and current February, as well as with March total precipitation and September SPEI-1(Fig. 4a, Table S2a). Further analysis in DENDROCLIM2002 revealed the strongest (P<0.05) correlations existed between the TRW chronology and temperature for months in the previous monsoon period (p August T_{min} (r = 0.725) and p June T_{mean} (r = 0.518)) (Table S3).

The longer TRW chronology (1946-2007) was correlated (P<0.05-0.01) with temperature for individual months during the previous post- and pre-monsoon seasons (p October-April), as well as with winter precipitation (p November to January) and moisture (p December-February) (Fig. 5, Table S4). Correlations with temperature variables were positive, and with precipitation and moisture were negative. DENDROCLIM 2002 indicated the strongest correlation (P<0.05) was between the TRW chronology and January SPEI-3 (r = -0.422) (Table S3; Figure S3).

Abies spectabilis height growth (HGI, 1993-2007) was significantly correlated with fewer climate variables compare to TRW. HGI was correlated with late monsoon (September) temperature (negative; T_{max} and T_{mean}) and p October total precipitation (positive), as well as previous monsoon and post-monsoon moisture conditions (p September-January) (Fig. 4b, c,

Table S2b). The strongest correlations identified by DENDROCLIM2002 included September T_{mean} (r = -0.627) and p October SPEI-6 (r = 0.629) (Table S3).

The relationship between the *C. fastigiata* AGI and LEAF chronologies and climate revealed moisture availability in the previous-year may be critical to stem elongation (p May to p July; Fig. 6a, Table S5a), and in the current year to leaf production (September; Fig. 6b, Table S5b). In addition, higher maximum temperature in previous year pre-monsoon (p May) positively influenced stem elongation (AGI). DENDROCLIM2002 showed the strongest relationships (P<0.05) exist between the AGI chronology and p May SPEI-12 (r = 0.817), and the LEAF chronology and p May SPEI-12 (r = 0.885) (Table S3).

3.3 High frequency chronology response to climate

Examination of the *A. spectabilis* and *C. fastigiata* chronologies on a year-by-year basis further support these climate-growth relationships. *A. spectabilis* radial growth (1993-2007) increased in 1993, 1995, 1999, 2001, 2003 and 2006 following years with higher mean temperatures in June (Fig. 7a). Radial growth declined in 1997, 2000 and 2002 following cooler Junes. Radial growth was similarly influenced by warmer p Aug T_{min} in 1996, 1999, 2001, 2006 and 2007 (Fig. 7b). When comparing the TRW and p June T_{mean} and p Aug T_{min} time series, the Gleichläufigkeit values were 61% and 75%, respectively, but sign tests were not significant (P>0.05) (Table S6).

For the longer *A. spectabilis* chronology-climate relationships (1946-2007), greater moisture availability in late autumn and winter (NDJ) was detrimental to radial growth (negative correlation) (Fig. 5). Radial growth declined in 1949, 1957, 1962, 1978, 1984, 1989 and 1998 following positive Jan SPEI-3 values (Fig. 8). Moving window analysis showed a significant (P<0.05) and consistent negative relationship between January SPEI-3 and the longer TRW chronology (Fig. S3). The Gleichläufigkeit value was 63%, but the sign test was not significant (Table S6).

Higher p October SPEI-6 values corresponded to higher HGI in 1997, 1999, 2000, 2002 and 2006, while lower p October SPEI-6 resulted in reduced HGI in 1993-1995, 1998, 2001 and 2004 (Figure 7c). Elevated late monsoon (September) temperatures showed lower HGI in 1994, 1998, 2001 and 2004 while lower mean temperatures at the end of the monsoon season resulted

in higher HGI in 1997, 1999, 2000, 2002, 2006, and 2007 (Figure 7d). Gleichläufigkeit values were 79 and 71% respectively, but the sign tests were not significant (Table S6).

Analyses of *C. fastigiata* AGI and LEAF response to SPEI, indicated that low growth in the years 2000, 2002, 2003 and 2007 corresponded to negative or minimally positive *p* May SPEI-12 values (Fig 7e, f). Increased AGI and LEAF growth in the years 1999, 2001, 2004, and 2005 aligned with positive *p* May SPEI-12 values. The Gleichläufigkeit values were 100 and 100%, respectfully and sign tests were significant (P<0.05) (Table S6).

4. Discussion

4.1. Chronology quality and development

The good chronology quality statistics of *A. spectabilis* TRW and HGI time series underline their dendroecological usefulness. In particular, high mean sensitivity in the HGI chronology indicates the responsiveness of sapling height growth to fluctuations in the environment. Comparison with *A. spectabilis* TRW chronologies from FTE sites in western (Sano et al., 2005) and eastern Nepal (Chhetri and Cairns, 2016) showed similar chronology quality statistics.

The mixed chronology quality statistics characterizing the *C. fastigiata* chronologies indicate moderate sensitivity to inter-annual variability in environmental conditions, with a lower degree of annual persistence. The EPS values fell below the recommended 0.85 threshold (Wigley et al., 1984), an indication that individual plant-level noise may be obscuring the stand-level signal. However, this study's chronology-quality statistics are comparable to two shrub-ring width *C. fastigiata* time series developed for sites on the Tibetan Plateau and the central Himalayas, Nepal (Liang et al., 2015).

4.2 Growth variable-specific response to climate

In the more recent past (1993-2009), *A. spectabilis* cambial growth may be responding to previous monsoon season conditions (e.g., elevated temperatures), allowing for the greater sequestration and translocation of non-structural carbohydrates and plant nutrients beneficial to radial growth in the following year (Renneberg et al., 2006). In years when monsoon season temperatures were lower (e.g., 1997, 1999), growth declined in the following year. Climatological evidence indicates increasing mean temperatures in all seasons and an earlier start

of the growing season (1982-2006) in the Himalayas in general, and in the high-elevation ecoregion of the present study (Shrestha et al., 2012). Thus, in the short term, longer and warmer monsoon seasons may be beneficial to *A. spectabilis* radial growth. Other dendroecological studies have noted the importance of temperature on radial growth at alpine sites during the growing season (Esper et al., 2003; Wang et al., 2005; 2006; Dang et al., 2009). However, given the short length of the TRW chronology (and others presented herein) and the potential for some climate variability, we suggest caution when interpreting results.

Over a longer period (1946-2007), the TRW-climate relationships revealed the detrimental influence of greater mid-winter moisture availability on radial growth. High January SPEI-3 may correspond to higher overall winter snowfall and a deeper snowpack, which can result in the delayed initiation of the growth and cambial activity through delayed snow melt (Vaganov et al., 1999; Rossi et al. 2008). Shrestha et al. (2015) also noted the negative influence of *p* December precipitation (i.e., snow) on radial growth. Our study also indicates a positive response to warmer winter temperatures as shown in other dendroecological studies in the Himalayas (Borgaonkar et al., 2009; Bräuning, 2004; Chhertri and Cairns, 2016). However, we did not detect the negative influence of lower moisture availability in the pre-monsoon season (MAM) on *A. spectabilis* TRW as recorded for sites in the western and central Himalayas (Borgaonkar et al., 1999; Sano et al., 2005; Tiwari et al., 2017) or previous summer temperature in the eastern portion (Gaire et al., 2017). This difference in response may be due to factors related to site conditions and climate. The mesic conditions of our study site might dampen the species sensitivity to pre-monsoonal moisture, particularly when compared to study sites on more xeric slopes or those located in the western Himalayas where moisture stress may be greater (Chhetri and Cairns, 2016). The influence of geography (i.e., latitude, elevation) and topography (i.e., slope, aspect) on site conditions in heterogeneous environments like the Himalayas is not insubstantial, and is not well quantified. These subtleties make dendroecological comparisons between sites and studies challenging. In addition, meteorological measurements (e.g., precipitation) and the climate models based upon them for these remote, high elevation sites are somewhat suspect given the low number of stations, their lower elevation and the short duration of the data sets.

Abies spectabilis HGI responded negatively to high temperatures in the late monsoon (September) and positively to *p* Oct precipitation and moisture (SPEI-1, -3 and -6). Lower

moisture during the initial post-monsoon month (October) and across the MJJASO period may result in reduced carbon sequestration used in height growth in the following year. During this period, moisture depletion at alpine sites in the Himalayas may occur due to high levels of evapotranspiration associated with higher temperatures and greater insolation (assuming warmer temperatures are associated with sunny skies, fewer clouds and lower precipitation). Low moisture availability may be further compounded in years of overall lower pre-monsoonal and monsoonal precipitation, as well as lower total snowpack, reduced snowpack extent and/or earlier melt and subsequent run-off from steeply sloped sites. The negative effect of elevated September temperatures on HGI may indicate the importance of late monsoon moisture conditions. This late-growing season response may also suggest that height growth continues throughout the entire monsoon season, a premise currently unexplored for mid-latitude alpine sites. If soil moisture becomes limited due to a shorter monsoon season, coupled with elevated temperatures, *A. spectabilis* may exhibit a moisture stress response by terminating height growth early. However, this hypothesis is only supported by the negative temperature-growth signal for September.

Contrary to other studies of boreal and montane conifer species (Pensa et al., 2005; Lindholm et al., 2010; Mathisen and Hofgaard, 2011; Wang et al., 2016) which show the positive influence of previous growing season temperatures on bud development and next year's shoot length, no response to temperature was detected other than the late-monsoon signal. This lack of response, aside from September, may indicate that higher temperatures during other times of the year are less influential on HGI, when compared to moisture availability. The response of *A. spectabilis* HGI to *p* Oct precipitation and moisture, and September temperatures is unique and further investigation is needed.

Lower available moisture in the previous year, including extreme hydroclimatic conditions such as drought, potentially limited current year *C. fastigiata* growth, both AGI and LEAF, at this high elevation site. The *C. fastigiata* growth chronologies were characterized by low growth in 2000 and 2002, following documented winter drought (DJF) conditions in the previous year (i.e., 1999, 2001) (Sigdel and Ikeda, 2010). Studies of *Betula utilis* tree-ring chronologies from the central Himalayas also indicated narrow or missing rings during these drought years (Dawadi et al., 2013; Liang et al., 2014). The response of *C. fastigiata* to previous year pre- and early-monsoon SPEI-12 may be indicative of a longer-term integrative effect of

moisture availability on photosynthesis, and as potentially regulated through stored carbon reserves made available from one year to the next.

In the limited number of shrub-based dendroecological studies in the region, both moisture (Liang et al., 2012) and temperature (Xiao et al., 2007; Liang and Eckstein, 2009; Li et al., 2013) signals have been reported, likely reflecting species-specific physiological responses to ecological (biotic) and environmental (abiotic) conditions. Studies of other *Cassiope* species in arctic and alpine environments have noted positive associations with temperature (Weijers et al., 2010; Rayback et al., 2012a, b). For sites on the Tibetan Plateau and the central Himalayas, Liang et al. (2015) reported *C. fastigiata* shrub-ring width chronologies were positively correlated with previous late winter/early spring temperatures, as well as previous autumn and current spring precipitation (Himalayan site only). The lack of agreement in climatic response of *C. fastigiata* in this and Liang et al.'s (2015) study may relate to differences in site moisture conditions, time period and climate variables investigated, and/or growth chronology studied (i.e., AGI vs. shrub-ring width). As only three *C. fastigiata* site chronologies currently exist for the region, further investigation of this and other Himalayan high elevation shrub species' response to environmental drivers are needed to clarify differences related to geography versus species physiology. Careful consideration of the multiple interactions between temperature, moisture (i.e., type, amount, timing) and site characteristics in alpine environments is critical to dendroecological studies, particularly over shorter periods; otherwise, subtleties of tree and plant responses may be smoothed over or missed entirely.

4.3 Concurrent examination of FTE tree and shrub species

By sampling co-occurring tree and shrub species, it is possible to move a step closer towards understanding the similarities and differences in climatic response between high elevation trees and shrubs, as well as the related physiological mechanisms that drive the local and regional landscape patterns of the forest-tundra ecotone (Li et al., 2014). In the Himalayas, rising temperatures (Shrestha et al., 1999), variable precipitation (Shrestha et al., 2012), a weakening monsoon (Wang and Ding, 2006; Zhou et al., 2008) and the minimally understood elevation-dependent warming phenomenon (Mountain Research Initiative EDW Working Group, 2015) could result in greater moisture variability in the future. Herein, we show that moisture availability was important for both tree and shrub growth in the FTE, either through positive

(HGI, AGI, LEAF) or negative associations (TRW, 1946-2007), but that the timing and surplus and/or deficit of moisture was unique for each species and chronology. It is hypothesized that greater future moisture variability in the Himalayas may result in potential periodic growth reductions, dieback and/or death of individual shrubs and trees (Liang et al., 2014). At the community level, if growth of *A. spectabilis and C. fastigiata*, in addition to co-occurring species such as *Betula utilis* (Liang et al., 2014), is limited by changes in moisture availability, particularly in the pre-monsoon and monsoon seasons, there is the potential for changes in the spatial distribution of vegetation within, and the location of, the FTE. Obviously, other anthropogenic, ecological and environmental factors, singly and in combination, will influence changes in the FTE (Holtmeier and Broll, 2005; Hofgaard et al., 2012; Gaire et al., 2014; Shrestha et al., 2015; Gaire et al., 2017). Additionally, *A. spectabilis* TRW (1993-2007) and HGI were mediated, both positively and negatively by previous and current monsoon season temperatures, respectively, in the recent past. These temperature-chronology relationships may be an initial harbinger of future response to monsoon season climate changes or may only be a manifestation of recent climatic variability. It is particularly noteworthy that temperature- and moisture-stress responses were noted for *A. spectabilis* (HGI) and *C. fastigiata* (AGI, LEAF) on a north-facing, mesic site as FTE sites on western and southern aspects tend to be warmer and drier. While some evidence (Shrestha et al., 2012) suggests that rising temperature and precipitation may positively influence vegetation growth in multiple ecoregions across Nepal, these projections may not be representative of all FTE sites in the Himalayas and, they may not account for the effects of anomalous climatic events such as drought (Richardson and Friedland, 2009).

5. Conclusion

Dendroecological evidence suggests that growth of co-occurring tree (*Abies spectabilis*) and dwarf shrub (*Cassiope fastigiata*) species at a FTE site in the central Himalayas (Nepal) is predominately influenced by previous pre-, monsoon and post-monsoon season climate conditions. For *A. spectabilis,* higher winter moisture limits TRW over the longer term (1946-2007). However, in the recent past (1993-2007), warmer temperatures in the previous monsoon season are beneficial to current radial growth. *A. spectabilis* HGI benefits from higher moisture availability in the late- to post-monsoon period of the previous year, but end-of-monsoon-season

warmer temperatures in the current year may limit growth if moisture is limited. Reduced moisture availability (SPEI-12) in the previous pre- and early monsoon also limits *C. fastigiata* growth (AGI, LEAF). This study contributes further evidence that moisture outside of the current monsoon season influences trees and shrub growth at the FTE at mid-latitude sites; a finding that refines our previous understanding that growth at arctic and alpine sites is primarily limited by growing-season temperature (Lloyd and Bunn, 2007; Körner, 2012). Within the context of both long-term decline (Sano et al., 2011) and more recent variability (Shrestha et al., 2012) in precipitation in the Himalayas, moisture availability may become a more frequent stressor of plant growth at high elevation sites under climate change, particularly if temperatures continue to rise (Shrestha et al., 1999; Practical Action, 2009). Investigations into whether *C. fastigiata* can provide longer chronologies to understand and reconstruct past moisture availability in the FTE are needed. Further, dendroecological examination of co-occurring tree and shrub species at the FTE can identify disparate and concomitant growth responses to climate drivers, thus providing information and insight into FTE change in the Himalayas and elsewhere.

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Figure legends

Fig. 1. a) Elevational map of study area with Lauribinayak study site (black triangle) and closest meteorological station (Dhunche, black circle). Inset maps: b) location of Langtang National Park in Nepal with red dots marking Climate Research Unit (CRU) (TS3.23 at 0.5° spatial resolution; 26.0 to 32°N, 78.0 to 90°E; Harris et al., 2014) grid points, and c) ecozones of Langtang National Park.

Fig. 2. Monthly mean temperature (T$_{mean}$, solid line) and total monthly precipitation (columns) for the Lauribinayak, Nepal study site. Meteorological data was derived from the CRU TS3.23 dataset for the 1978-2007 period (30 year mean).

Fig. 3. An example of visual crossdating of four live *Cassiope fastigiata* stems from a single plant (TLC10). Annual growth increments (AGI) are identified by the dashed vertical lines and the calendar year is noted directly below. For the entire dataset, average within-plant correlation was r = 0.75 (TLC10 range: r = 0.67-0.80; dataset range: r = 0.60-0.90).

Fig. 4. Spearman's rank correlation coefficient between climate variables and *Abies spectabilis* a) tree-ring width, and b) and c) height growth increment chronologies (1993-2007). Climate variables include mean minimum temperature (T$_{min}$), mean maximum temperature (T$_{max}$), mean temperature (T$_{mean}$), total precipitation (PRCP), and the Standardized Precipitation-Evapotranspiration Index (SPEI-1, -3, 6; Vicente-Serrano et al., 2010) for the previous May to the current October. Dashed line represents P<0.05.

Fig. 5. Pearson's correlation coefficients (r) between climate variables and *Abies spectabilis* tree-ring width (1946-2007). Climate variables include: a) mean minimum temperature (T$_{min}$), mean maximum temperature (T$_{max}$), mean temperature (T$_{mean}$), and b) total precipitation (PRCP) and the Standardized Precipitation- Evapotranspiration Index (SPEI-1, -3, 4; Vicente-Serrano et al., 2010) for the previous May to the current October. Dashed line represents P<0.05.

Fig. 6. Spearman's rank correlation coefficient between climate variables and *Cassiope fastigiata* a) annual growth increment, and b) annual production of leaves chronologies (1999-2007). Climate variables include: a) Standardized Precipitation- Evapotranspiration Index (SPEI-12;

Vicente-Serrano et al., 2010) and b) SPEI-12 and total precipitation (PRCP) for the previous May to the current October. Dashed line represents P<0.05.

Fig. 7. Comparison of climate variables with *Abies spectabilis* (1993-2007) tree-ring width (TRW) (a-b) and height growth increment (HGI) (c-d) chronologies and *Cassiope fastigiata* (1999-2007) annual growth increment (AGI) (e) and annual production of leaves (LEAF) (f) chronologies. Climate variables include: a) previous June mean temperature (T_{mean}), b) previous August minimum temperature (T_{min}), c) previous October Standardized Precipitation Evapotranspiration Index (SPEI-6; Vicente-Serrano et al., 2010), d) September mean temperature, and e-f) previous May SPEI-12.

Fig. 8. Comparison of *Abies spectabilis* (1946-2007) tree-ring width (TRW) chronology with the January Standardized Precipitation Evapotranspiration Index (SPEI-3; Vicente-Serrano et al., 2010).
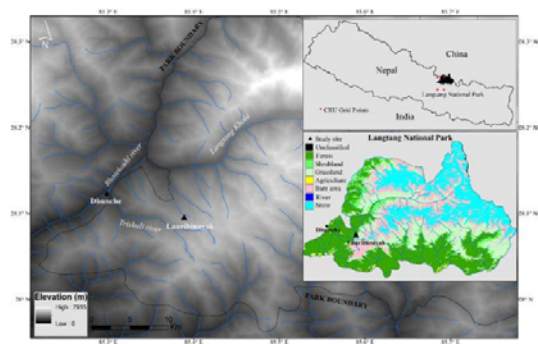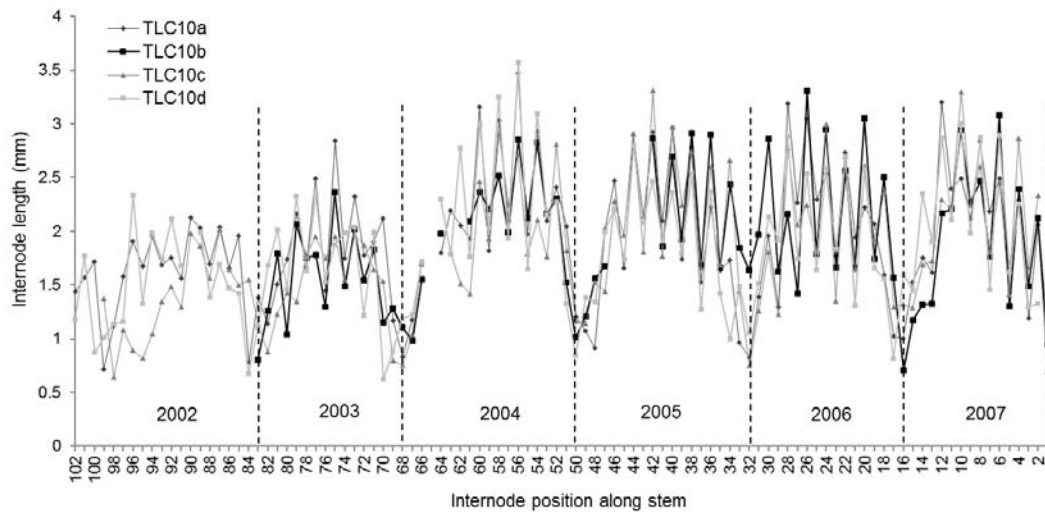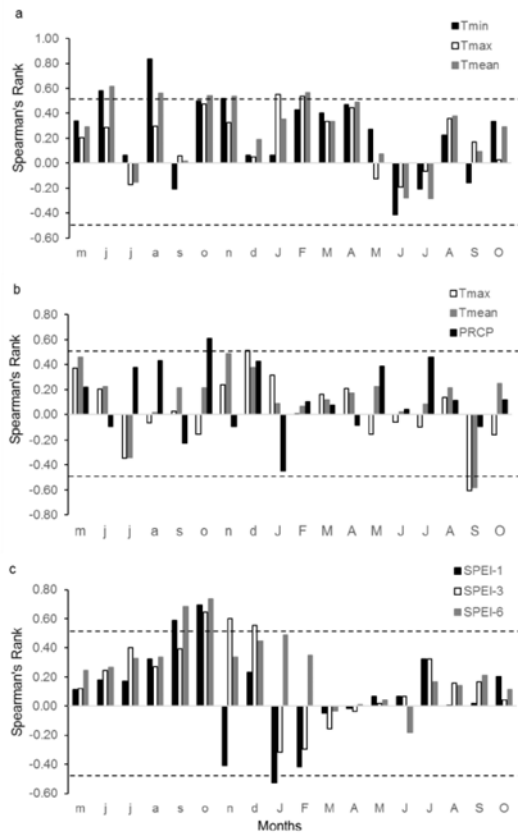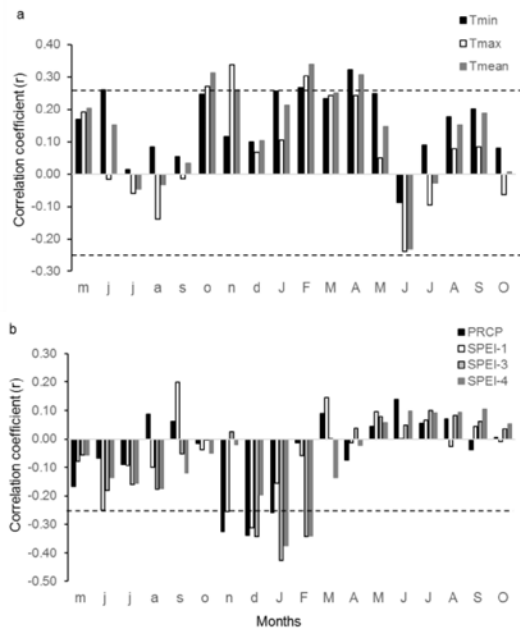
Fig. 1
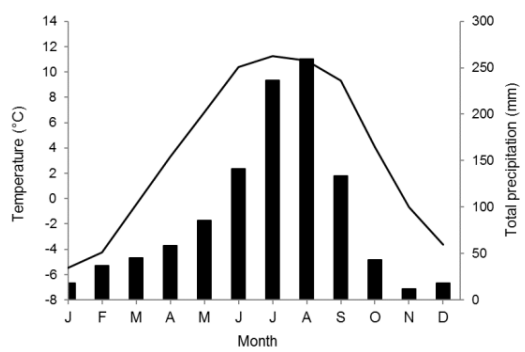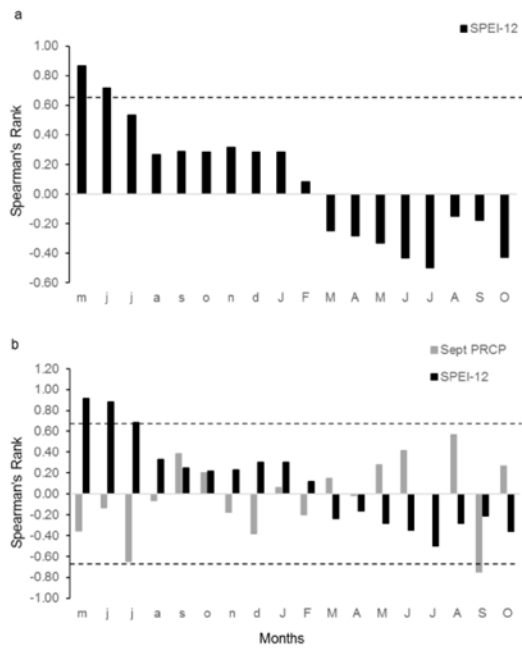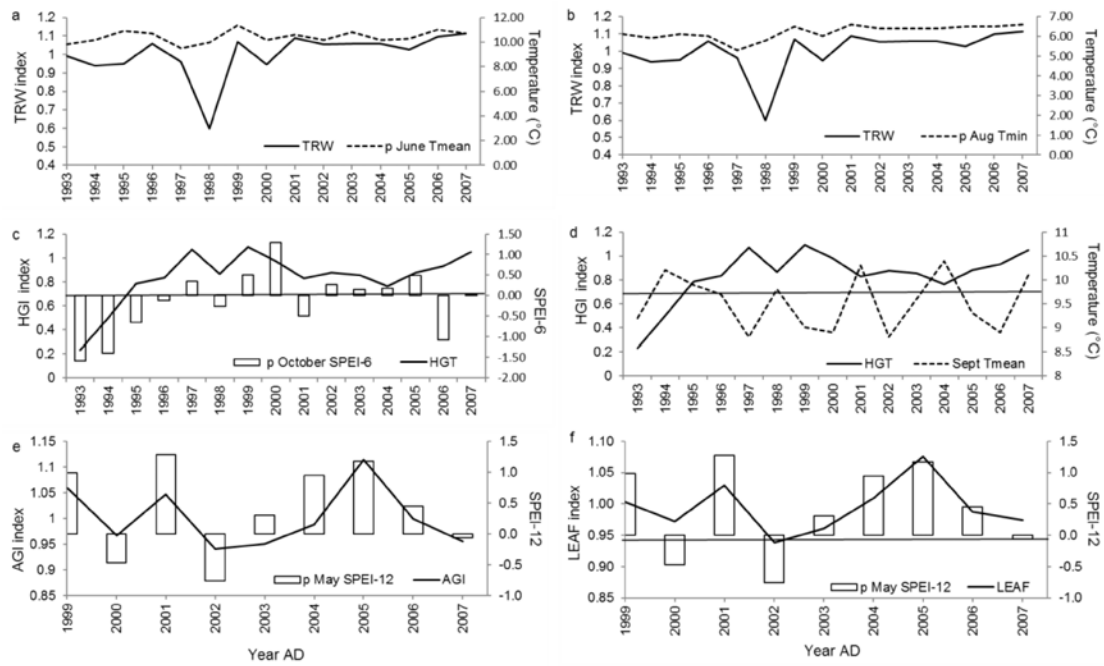
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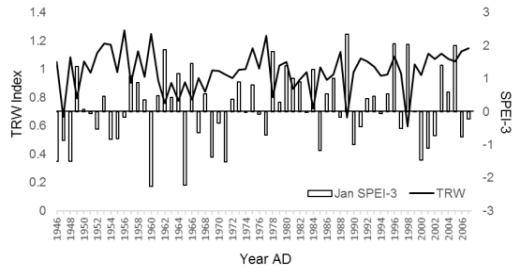
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Fig.8.

Table

Table 1. *Abies spectabilis* and *Cassiope fastigiata* chronology statistics based on COFECHA output.

	Abies spectabilis		Cassiope fastigiata	
	TRW[a]	HGI[b]	AGI[c]	LEAF[d]
Chronology Length	1946-2007	1993-2007	1999-2007	1999-2007
Number of Years	62	15	9	9
Total number of trees or plants	24	60	25	25
Total number of cores or stems	35	60	44	42
Series intercorrelation	0.56	0.40	0.46	0.52
Mean sensitivity	0.24	0.42	0.20	0.16
First-order autocorrelation	0.78	-0.02	-0.25	-0.27

[a]TRW: *Abies spectabilis* tree-ring width chronology

[b]HGI: *Abies spectabilis* height growth increment chronology

[c]AGI: *Cassiope fastigiata* annual growth increment chronology

[d]LEAF: *Cassiope fastigiata* total number of leaves produced per year chronology