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Tree-growth response to climatic variability in two climatically contrasting treeline ecotone areas, central Himalaya, Nepal

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Abstract:

Tree growth at the treeline ecotone is known to be sensitive to climate variability, and is thus considered a world-wide bio-monitor of climate change. However, our understanding of within-region variation in growth responses through space and time is limited. A dry south-facing slope dominated by *Pinus wallichiana* and a wet north-facing slope dominated by *Abies spectabilis* in Nepal, central Himalaya, were used to analyze the inter-site (i.e., dry vs. wet sites) and intra-site (i.e. treeline vs. forest line elevations) tree-growth relationships, as well as response to monthly and seasonal temperature and precipitation at annual and bi-decadal time scales. At both study sites, and at two elevations within each site, growth can be strongly affected by growing-season and non-growing-season factors, however, there are inconsistencies in terms of the climate-growth relationship across space and over time. At the dry site, only a weak positive growth response to summer temperature is observed. At both sites, there is a negative growth response to winter precipitation at both high and low elevations, and this response is markedly independent of the summer and winter temperature trends of the respective site. At the wet site, growth at the higher elevation is negatively correlated to early summer temperature, whereas a positive growth response to spring precipitation is observed at the lower elevation, indicating a possible drought effect. The results illustrate how different climatic drivers may govern tree-growth responses both between sites with contrasting climates within a region, and along elevational gradients within the treeline ecotone. This underlines the need for multi-scale studies, and a focus on multiple climate variables, when analyzing treeline ecotone responses to climate change.

23 Introduction

24 The treeline ecotone, which marks the transition from closed forest to the treeless alpine or
25 arctic tundra, is highly responsive to climate (Germino et al. 2002; Dullinger et al. 2004;
26 Holtmeier and Broll 2005) and regarded as a sensitive world-wide biomonitor of past and
27 recent climatic variability (IPCC 2007). Response of the treeline ecotone to climate change
28 can be observed in terms of changing tree growth, recruitment, and species composition
29 (Szeicz and Macdonald 1995; Hofgaard 1997; Paulsen et al. 2000; Camarero and Gutierrez
30 2004; Hofgaard et al. 2009). These structural parameters are influenced by multiple abiotic
31 factors (e.g. temperature, precipitation, slope exposure, radiation, wind, moisture) including
32 factors outside the growing-season (Paulsen et al. 2000; Holtmeier and Broll 2005; Wang et
33 al. 2006; Li et al. 2008; Aune et al. 2011; Mathisen and Hofgaard 2011).

34 At high-elevation sites worldwide tree growth is considered to be strongly limited by
35 temperature and a positive growth response to summer temperature is commonly observed
36 (Villalba et al. 1997; Cullen et al. 2001; Körner 2003; Bhattacharyya et al. 2006). However,
37 the tree growth–temperature relation is not a constant factor through time and space (Morales
38 et al. 2004; Dang et al. 2009; Fang et al. 2009; Gruber et al. 2009). The influence of summer
39 temperature generally increases with increasing elevation and is typically important near the
40 treeline – the uppermost elevation marked by a single upright tree individual (Villalba et al.
41 1997; Barber et al. 2000; Paulsen et al. 2000; Takahashi et al. 2003; Wang et al. 2005). This
42 elevational change in summer temperature sensitivity, combined with precipitation impacts
43 (Biondi and Waikul 2004; Morales et al. 2004), and impacts by non-growing-season climate
44 factors, causes a multitude of tree-growth response patterns across time and space (Grace and
45 Norton 1990; Kullman 2007; Huang et al. 2010; Mathisen and Hofgaard 2011).

46 In general agreement with the global trend, the Himalayan region has experienced
47 rising temperatures over recent decades (IPCC 2007). In Nepal, the average temperature

increased by 0.6°C between 1976 and 2005 (Practical Action 2009). A monsoon climate system and complex topography dominated by high mountains causes strong local to regional scale climate variability (Cook et al. 2003). Trends in climate change also vary across the Himalaya, for example rates of temperature change increase towards high-elevation areas (Shrestha et al. 1999). Furthermore, the timing of key climate events, such as the onset of the monsoon (Xu et al. 2009), also varies through time with strong repercussions for tree growth (Vaganov et al. 2006). This climatic complexity provides opportunities for studying the variability in climate–growth relationships in climatically contrasting treeline ecotones within the same geographical region. While the effect of geographic variability on monsoon climate systems *per se* has been extensively studied worldwide (Therrell et al. 2002; Biondi and Waikul 2004; Bräuning and Mantwill 2004; Morales et al. 2004), studies explicitly linking tree-growth response to climatic variability in time and space at high-elevation sites in regions such as the Himalaya, where the monsoon is a key climatic factor, are less well studied (but see; Cook et al. 2003; Sano et al. 2005; Bhattacharyya et al. 2006; Singh et al. 2006; Shah et al. 2009; Tenca and Carrer 2010; Borgaonkar et al. 2011).

The treeline ecotone in the Nepalese Himalaya is dominated by *Abies*, *Pinus*, *Juniperus*, and *Betula* species, depending on aspect and local climatic factors. In this study, we focus on two conifer tree species dominating two climatically contrasting treeline ecotones of central Nepal: Himalayan blue pine (*Pinus wallichiana* A. B. Jacks.) as representative of semi-arid south-facing slope conditions and Himalayan fir (*Abies spectabilis* (D. Don) Spach) as representative of wet north-facing slope conditions. The following questions are addressed in the study: (1) How does tree radial growth respond to climatic variability along an elevational gradient (i.e. across the treeline ecotone), and does the response vary between climatically different sites (dry vs. wet environments)? (2) Does the growth response vary over time (i.e. between decadal periods), and if so, what is driving this variability? To answer

these questions tree-ring chronologies representing two climatically contrasting areas were selected, and two different elevations representing the lower and upper zone of the treeline ecotone were studied at each site. Tree radial growth was then tested for correlation with monthly and seasonal temperature and precipitation variables (assessed from the nearest stations) for different periods.

Methods

Study areas

The study was carried out in two sites in subalpine areas of central Nepal, in the central part of Himalaya (Fig. 1): Ngawal (28°38'N, 84°06'E; hereafter DRY) in the Manang district of the Annapurna Conservation area and Lauribinayak (28°05'N, 85°22'E; hereafter WET) in the Rasuwa district of the Langtang National Park. The treeline ecotone extends between approximately 3700 and 4200 m a.s.l. with a somewhat wider elevational range in DRY (approx. 3930-4180 m a.s.l.) than in WET (approx. 3770-3950 m a.s.l.). The average stand height at the forest line at DRY is 9 m and at WET 14 m. The average DBH at forest line and treeline at DRY is 35 cm and 10 cm, respectively, whereas at WET it is 39 cm and 17 cm, respectively. The landscape of the dry site is characterized by glacial and interglacial deposits (Hagen 1969), whereas the wet site is dominated by rock-fall sediments and glacio-fluvial moraine deposits (Heuberger et al. 1984). The high-elevation subalpine forests are dominated by *Pinus wallichiana* at DRY and *Abies spectabilis* at WET. At DRY, the pine is mixed with *Juniperus* sp. throughout the treeline ecotone, whereas at WET, the forest, is composed of *A. spectabilis*, *Betula utilis* D. Don, and *Rhododendron campanulatum* D. Don. Both sites are impacted by disturbance from nearby human settlements (grazing, trampling, and harvesting of firewood, timber, litter, and medicinal plants). The disturbance is less intense at DRY despite closer proximity to human settlement, possibly because conservation regulations are more effectively implemented due to the involvement of local monks in this area.

98 **Field sampling**

99 The field investigation was conducted from June-July 2008 (*Abies spectabilis*, WET) and
100 2009 (*Pinus wallichiana*, DRY). At each site the sampling included two different elevations
101 of the treeline ecotone (Table 1): forest line representing the lower part of the ecotone, and
102 treeline representing the upper part. The forest line is defined as the uppermost elevation
103 where closed stands of trees are found, the treeline as the uppermost elevation where
104 individual trees are found (>2 m). At each site and elevation, a minimum of 20 healthy and
105 dominant *Pinus/Abies* individuals were selected and cored with a 5 mm increment borer in
106 two opposite directions at a height of 50-80 cm. Most of the *Pinus wallichiana* trees in DRY
107 were multi-stemmed, and when so, the dominant living stem was selected for coring.

108 **Chronology development**

109 Cores were mounted on wooden supports and the rings made visible by using sandpaper,
110 scalpel and zinc ointment. Ring width was measured to an accuracy of 0.01 mm using an
111 electronic analysis bench (LINTAB; TSAP; Heidelberg, Germany) and a binocular
112 microscope. Cores were visually and statistically cross-dated to identify possible false rings,
113 missing rings or measurement mistakes using COFECHA (Holmes 1983). Cores with low
114 correlation with the main chronology ($r < 0.5$), or that had rotten parts, were discarded from
115 further analyses. In total, 86 trees (range 18-24 per site and elevation) were analyzed. The ring
116 width of sampled trees generally decreased with age and was thus detrended with a negative
117 exponential curve or a straight line (Software Program ARSTAN Version 44D; Cook et al.
118 2012). The detrended series were pre-whitened by removing autocorrelation from each series
119 using an autoregressive moving average time-series model to produce residual chronologies
120 that emphasize high-frequency, year-to-year variations (Cook 1985). Mean site index values
121 for each year were calculated using the bi-weight robust mean method (Cook and Kairiukstis
122 1990). The quality of the resulting residual chronologies was assessed on the basis of

statistical parameters: standard deviation (SD), expressed population signal (EPS), and mean sensitivity (MS) (Fritts 1976). High mean sensitivities, expressed population signal, and series inter-correlations in the tree-ring chronologies indicate a high dendroclimatic potential of the species (Cook and Kairiukstis 1990). Residual and standard chronologies were constructed for each analyzed elevation per study site. The residual chronologies were used for studying growth characteristics and the standard chronologies were used in the during climate-growth relationship analyses. The longest chronology runs from 1905 (forest line) at WET (Table 1), and the maximum common interval among all the chronologies is 1968-2007.

Climate data

The climate in the central Himalaya is monsoon-dominated with an east to west precipitation gradient, resulting in drier climates in the west (Shrestha 2000). Moist southerly winds bring heavy precipitation during the monsoon period (mainly June-August), but rugged topography and mountain barriers create rain-shadow regions with limited rainfall. In the climate-growth relationship analyses we used climate data available from the nearest stations that could provide reliable and complete (i.e., no missing data) monthly temperature and precipitation data covering as much of the period for which tree growth data were available. These stations were Chame (at 2680 m; ~17 km south-east from DRY), and Kathmandu (1336 m; ~44 km south from WET) (Table 2), which provide monthly temperature and precipitation data over the period 1978-2007. The annual precipitation at Chame (969 mm) is ca. 66% that of the Kathmandu station (1466 mm) (Table 3; Fig. 2 a and b). The annual mean temperature at Chame is 10.4°C and 18.6°C for Kathmandu (Table 3). January and July are the coldest and the warmest months respectively, at both stations (Fig. 2a and 2b). Snow is common in the winter and lasts for about five months (November-March) in both study sites, but may extend sometimes into early May. The proportion of annual precipitation that falls as snow is higher in DRY (26% of the annual precipitation) than WET (below 10% of the total annual

precipitation). Warm dry summers, in combination with frequent strong winds, produce more xeric conditions in DRY relative to WET where lower temperatures and high precipitation during summer create wetter conditions.

The mean annual temperature record at Chame (representing the DRY site climate for 1978–2007) reveals a significant increasing trend ($0.03^{\circ}\text{C}/\text{year}$), but none of the seasonal mean monthly temperatures shows significant change over the same period (see Fig. 2d for p -values). Mean temperatures at Kathmandu (representing WET) show a significant (see Fig. 2d for p -values) increasing trend across all seasons individually and taken together (autumn (SON) $0.06^{\circ}\text{C}/\text{year}$; winter (DJF) $0.07^{\circ}\text{C}/\text{year}$; spring (MAM) $0.06^{\circ}\text{C}/\text{year}$; summer (JJA) $0.02^{\circ}\text{C}/\text{year}$; annual $0.06^{\circ}\text{C}/\text{year}$). Precipitation data from both stations (Chame and Kathmandu) show no trends for the 1978–2007 period (Fig. 2 e and f).

Lapse rate estimation and verification of climate data

Temperature estimates were calculated based on data from Chame and Kathmandu. Firstly, mean monthly regional lapse rates were estimated based on temperature data from the nearest eight climate stations (to both Chame and Kathmandu) from which >10 years of continuous data were available. These stations ranged in elevation between 1982 and 4091 m a.s.l. Estimated regional lapse rates from these stations are $0.60^{\circ}\text{C}/100\text{ m}$ (January), $0.56^{\circ}\text{C}/100\text{ m}$ (May), $0.52^{\circ}\text{C}/100\text{ m}$ (July), and $0.57^{\circ}\text{C}/100\text{ m}$ (annual), and estimated temperatures based on these lapse rates are presented in Table 3. Besides the coldest (January) and warmest (July) months, May is included in the example as it represents the starting month of the monsoon, a key climatic factor in the region, but calculations were done for all monthly data. Based on these regional monthly lapse rate calculations, we estimated monthly mean temperatures for each study site, elevation and year (i.e., forest line and treeline at DRY and WET for each month in the period 1978–2007). The applicability of these estimated temperature data for use in the climate-growth analyses were verified for WET by correlating estimated values with

temperature data recorded by temperature loggers (Gemini Data loggers version 2.3; Type Tiny tag +12) installed at 2 m above the ground at the forest line at the start of the study (in 2008). Pearson correlations were calculated for (i) daily temperature data for 2010 and 2011 (Table 4), and (ii) monthly mean of temperatures for 2008-2011 (Fig. 2g). Results of these verification procedures show that both the monthly temperature variability over years, and the daily temperature variability within years, are relatively consistent between the loggers and the climate station data (see Figure 2g and Table 4).

We used precipitation data available from Kathmandu in order to maintain consistency in terms of stations used, even though the available Dhunche precipitation time-series length was able to cover the analysis period (1978–2007). The applicability of using precipitation data from Kathmandu was verified by correlating annual and monthly data to the data available from Dhunche over the analyzed period (1978–2007). The result showed that monthly precipitation variability was relatively consistent over time between the Kathmandu and Dhunche climate stations (see Fig. 2g and Table 4). Even though the actual temperature and precipitation values differ between the study site and the climate station, the estimated data generated from applying the lapse rate to the Kathmandu data adequately reflect the climatic variability of the study elevations over time (months and years).

Climate-growth analysis

Growth responses of *Pinus wallichiana* and *Abies spectabilis* to climatic variability were analyzed by correlation function analyses (Briffa and Cook 1990) using the *bootRes* package (Zang and Zang 2009; Zang and Biondi 2013) within the statistical software program R 3.1.2 (R Core Team 2008). *bootRes* is a very popular package for dendroclimatic calibration, modeled closely after *DENDROCLIM2002* (Biondi and Waikul 2004). The correlation function analysis is a regression approach where the tree-rings are modeled as a function of the climatic variables (Christiansen 2010). In our analysis, non-prewhitened standard tree-ring

chronologies were correlated with monthly climatic data (mean monthly temperature and total monthly precipitation) using Pearson correlations.

A 12-month span was used in the moving window correlation analyses (Biondi and Waikul 2004), including climatic data from September_{*t-1*} (the year prior to growth) to August_{*t*} (year of growth) over the 20-year analytical window between the years 1978 and 2007. This is the best fit maximum time-window accepted by the software (*bootRes* package) for the designated parameters. The period (1978-2007) represents the maximum time interval in common for tree-ring chronologies and station climate data for the two study elevations (within sites) and the two sites.

Results

Chronology comparison

Mean sensitivity increases towards higher elevation at both study sites, and the values are similar for all chronologies except the forest line at WET. There is no elevational trend in the series inter-correlation at DRY. Within each site there is a tendency for weak positive correlations between chronologies of the two elevations, but this is only statistically significant ($p < 0.05$) in WET for the analytical window 1978-2007 (Table 5). The forest-line chronology from DRY shows a significant positive correlation with chronologies from a previous study by (Cook et al. 2003) at Ngawal (28°39', 84°5', 3300 m) ($r = 0.72$; $p < 0.001$) and Pisang (28°37', 84°10', 3000 m) ($r = 0.59$; $p < 0.001$) for the common overlapping period (1968-1996) (See Table 5).

Both DRY chronologies show a markedly reduced growth in 1992 (Fig. 3). After this, growth increases at both elevations for a few years (up to 1995), but then the pattern diverges, with marked reduced growth recorded for 2001 and 2004 at the forest line, and for 1997 only at the treeline (Fig. 3). At WET, the different elevations show a more or less congruent

pattern up to 1997, with reduced growth at both elevations in 1984 and 1989. In 1998 and 1999 there is a somewhat reduced growth at the treeline and forest line, respectively (Fig. 3).

Climate–growth relationship

The correlation analysis of the climate-growth relationship over the full period (1978-2007) as well as for 20-year windows reveals significant growth responses to temperature and/or precipitation for all chronologies (Table 6). These responses were generally inconsistent for the full and all 20-year moving-window periods across the two sites (Fig. 4, Table 6), but the two sites share tendencies for negative growth responses to winter precipitation (December_{*t-1*} – February_{*t*}, with the forest line at DRY being the exception), as well as for generally positive growth responses to spring precipitation at the forest line, and for stronger climate-growth relationships at the treeline than at the forest line.

Apart from these similarities, the general pattern that emerges is a number of inconsistent and even contrary growth responses to the analyzed climatic variables at the two study sites, elevations, and over time. For the *Pinus wallichiana* population at DRY, tree growth at the forest line is positively correlated with September_{*t-1*} temperatures and April_{*t*} precipitation, but negatively correlated with January_{*t*} precipitation (Fig. 4, Table 6). These climate-growth correlations are generally consistent over most of the time periods. At the treeline of the same site, the only significant correlation is with precipitation in February_{*t*}, and this correlation becomes stronger over time (Table 6). For the *Abies spectabilis* population at WET, tree growth shows some consistency in positive growth responses to July_{*t*} temperature, but this was only significant over the full period (Fig. 4, Table 6). There were also negative growth responses to autumn temperatures at both elevations (October_{*t-1*} at forest line and September_{*t-1*} at treeline) and these correlations also weaken over time at both elevations. Inconsistencies between elevations are also found; tree growth at the forest line is positively correlated to spring precipitation (March_{*t*}, April_{*t*}), but these correlations disappear in the later

part of the study period. At the treeline, a growth response to May_t precipitation is consistently negative over time (Table 6), but this relationship becomes weaker when the time scale is extended to the full period (Fig. 4). Similarly, a strong negative influence of early summer temperature (June_t), observed in the shorter windows, disappears in the full period. At the same study elevation, growth responses to temperature show large monthly and time-window variations. In the early part of the period, there are negative growth responses to June_t temperature whereas in the later parts, significant positive correlations to March_t , July_t , and August_t temperature are observed (Table 6).

Discussion

Our comparative study of tree-growth responses across the treeline ecotone in two climatically contrasting Himalayan landscapes reveals clear climatic signals with considerable spatial and temporal variability. The main climatic drivers of tree growth vary between study sites, study elevations, and analytical windows, as discerned by annual and 20-year moving averages. Furthermore, growing-season as well as non-growing-season factors are found to significantly affect tree growth at both study sites, but there is little overall consistency in terms of specific climatic factors or temporal patterns. Tree growth shows a strong association with winter precipitation at the dry site and with spring (March_t , April_t) climatic variables at the wet site, both indicating the importance of non-growing-season climate, and in particular the timing of the onset of the monsoon at the wet site (see below).

A positive growth response to summer temperature is reported from many treeline ecotone regions world-wide, including Himalayan mountain forests (Esper et al. 2003; Wang et al. 2005; Wang et al. 2006; Dang et al. 2009; Shah et al. 2009). We find such positive growth responses to summer temperature at the wet *Abies spectabilis* site, though only for July_t temperature, and only when analyzed over the full analytical period. In the dry *Pinus wallichiana* site, summer temperature has only weak correlations with growth; a slight

positive correlation (not significant) is detected but only at the forest line and only in the later decades. Such weak or non-existent responses of tree growth to summer temperature could suggest that the interpolated climate data from Chame do not represent the climate of the study site and/or elevations very well. However, 2001 and 2004 were particularly poor growth years at the forest line of the dry site, and these were characterized not only by cold summers, but also by relatively high spring temperatures and low spring precipitation. It is thus possible that spring drought may have acted as an additional growth-limiting factor at this site, obscuring the summer temperature effect.

At the wet *Abies spectabilis* site, we find a consistent negative growth response to early summer (June_t) temperatures across all decades during the analyzed periods at the treeline elevation. This contradicts the commonly-observed positive growth response to summer temperature reported from many treeline ecotone regions world-wide, including the Himalaya (Esper et al. 2003; Wang et al. 2005; Wang et al. 2006; Lloyd and Bunn 2007; Dang et al. 2009; Shah et al. 2009), and also seems inconsistent with the positive growth response to July_t temperature found at the same site. Growth reductions under above-average growing-season temperatures in temperature-limited systems (including many alpine and arctic treeline ecotones) are often attributed to drought events or drought periods (Barber et al. 2000; Kirchhefer 2001; Lloyd and Fastie 2002; Wilmking et al. 2004), and such relationships could potentially explain the negative growth response to temperature in our *Abies spectabilis* site. This interpretation is corroborated by positive growth responses to spring precipitation at the forest line of this site (see below). It should be noted, however, that for June_t temperatures, the correlation between the station climate data (used in the analyses) and locally recorded temperature was low. The correlation was based on few observations, and this questions the validity of the temperature-growth relationship for this month. June belongs to the monsoon period at this site, and it is possible that our temperature-based lapse rate calculations are less

successful in capturing the actual climatic conditions at the site in months with high relative humidity (Dawadi et al. 2013; An et al. 2014; Liang et al. 2014).

A characteristic of the Himalayan climate is the quickly rising temperatures from March through to May, with the monsoonal precipitation lagging behind by some months, resulting in potential for water deficit (cf. Sano et al. 2005). At the forest line of our wet site, the potential importance of drought in explaining the negative spring temperature response is supported by a concomitant positive spring (March_{*t*}, April_{*t*}) precipitation response, and by the fact that this response is especially prominent during the drier earlier decade.

At the treeline of the wet site, the negative growth response to summer temperature coincides with a negative winter (December_{*t-1*}) and spring precipitation (May_{*t*}) response. The latter response was especially prominent during the wetter later decades, suggesting that spring drought is not limiting tree growth at the higher elevations of this site. In the Himalaya, a warm June is linked to an early onset of the monsoon, and at these elevations, part of this early monsoon precipitation may fall as snow, which may contribute to delayed snowmelt and hence late onset of the growing season. The date of cambial initiation, an important climate-linked process related to tree-ring growth, is known to be affected by the date of snowmelt, winter precipitation and soil warming (Worrall 1983; Kirdyanov et al. 2003). Furthermore, high precipitation implies increased cloudiness, leading to a significant reduction of soil temperature through reduced radiation input or high cloud albedo (Takahashi et al. 2005), which may also delay the soil warming in spring and hence contribute to reduced tree growth. These factors may help explain the extremely reduced growth event in 1998 when May precipitation was very high (highest among all the analyzed years; 282 mm vs. average May precipitation for analyzed period of 129 mm). Along the same lines, the negative growth response to high winter (December_{*t-1*}) precipitation at the treeline might also be attributed to delayed snowmelt or late onset of the growing season, due to high snow accumulation during

high winter precipitation years (Peterson et al. 2002). Thus, the severely reduced growth at the treeline and forest line in the event years 1989 and 1998 could be related to the high winter precipitation (December_{*t-1*}) in these years (137 mm in 1989; 116 mm in 1998; average for analyzed years, 54 mm) resulting in a severely delayed onset of the growing season.

Changes in the non-growing-season climate (viz. winter, spring, autumn temperature and precipitation) are main features of the recent climate change across the Himalaya (IPCC 2007; Practical Action 2009). Our results indicate that variation in these factors may have a strong, and differential, impact on tree growth across the treeline ecotone. A negative growth response to winter (January_{*t*}) temperature at the forest line in the dry *Pinus wallichiana* site might be associated with snow-pack accumulation. Generally, in colder winters, a higher proportion of the annual precipitation falls as snow and leads to increased accumulation. The recorded increased growth after cold winters could thus be mediated by melt-water from the snow-pack as an additional water source providing suitable conditions for an early onset of the growing-season in dry areas (Vaganov et al. 1999; Bekker 2005). However, such a response is not consistent across all analytical periods (except weak correlations in the later decades), suggesting the influence of decadal climatic variability and/or other event-year factors. Furthermore, such a negative growth response to winter (January_{*t*}) temperature at the dry site, is only detected in the later analytical windows when winter temperatures are more variable and generally warmer compared to earlier periods. At this site, warm winters may have reduced snow-cover duration which affects moisture availability during the following growing season (Beniston 2005).

In conclusion, these results illustrate how tree growth is defined by both temperature and precipitation variation during both the non-growing season and the growing season, but also by climate factors regulating moisture availability and length of the growing season. In the Himalayan treeline ecotone areas, the timing of the onset of the monsoon season is an

essential growth-regulating factor with a somewhat variable influence in dry and wet areas. An early monsoon (i.e., high rainfall in May) terminates the generally dry spring season and thus precludes early growing-season drought events. However, at the upper elevations of our wet area, tree growth appears to be primarily hampered by an early monsoon throughout the analytical period, and in some cases, such an effect can be tracked down to particular event years.

Our results illustrate that climate differences between focal areas and the importance of monsoon vs. non-monsoon seasonal variables vary through time, due to temporal and spatial variation in individual climate variables. Detailed analyses of event years and short time periods vs. longer periods can assist in improving scenarios and understanding processes regulating treeline ecotone responses to climate change. Even though our study only considers a restricted time period it underlines the need for a network of sampling areas in alpine treeline ecotone regions to identify the complex growth response to climate and the need to pay closer attention to multiple climatic drivers with deviating influence at a range of temporal and spatial scales.

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552

553 **Table 1.** Characteristics of sampled locations at the two study sites, sampled data, and constructed residual chronologies.

554

Study areas	Elevation range (m asl)	Chronology length (years)	No. of trees (cores)	Series inter- correlation	Mean sensitivity	Expressed Populatio n Signal (EPS)	Auto -correlation*	AR model*
<i>Pinus wallichiana</i> , DRY								
Forest line	3930-3965	1920-2008	21 (41)	0.51	0.23	0.96	0.65	1
Treeline	4015-4120	1960-2008	18 (31)	0.50	0.25	0.85	0.54	2
<i>Abies spectabilis</i> , WET								
Forest line	3770-3805	1905-2007	23 (35)	0.42	0.17	0.91	0.82	1
Treeline	3820-3910	1936-2007	24 (35)	0.56	0.24	0.94	0.78	1

555

556 * Statistics refer to variation in standard chronology; AR = Auto regressive.

557 **Table 2.** Characteristics of climate stations used for the climate-growth analyses and for climate data verification.

Study areas	Stations	Climate data	Elevation (m a.s.l.)	Latitude	Longitude	Available period
<i>Pinus wallichiana</i> , DRY	Chame	Temperature/Precipitation	2680	28°33'	84°14'	1977-2007
<i>Abies spectabilis</i> , WET	Dhunche*	Precipitation	1982	28°06'	85°18'	1971-2007
	Kathmandu	Temperature	1336	27°42'	85°22'	1968-2007
	Kathmandu	Precipitation	1336	27°42'	85°22'	1971-2007

558 *Station lacks sufficiently long temperature time-series and is only used only for climate data verification

Draft

Table 3. Overview of the climate at forest line and treeline elevations of the study sites. Temperature data (°C) for the coldest (January), the warmest (July) and monsoon onset (May) months are extrapolated from the Chame and Kathmandu climate station data for the period 1978–2007 based on regional monthly lapse rate calculations (see Methods for details). Min = mean of daily minimum values; Max = mean of daily maximum values.

Study sites / Climate stations	Elevation (m a.s.l.)	Temperature (°C)										Precipitation (mm)	
		January			May			July			Annual Mean	Annual	Summer JJA
		Min	Max	Mean	Min	Max	Mean	Min	Max	Mean			
<i>Pinus wallichiana</i> , DRY/Chame	2680	-2.3	10.0	3.5	7.9	20.2	13.2	10.2	20.4	15.3	10.4	969	470
Forest line	3930	-9.8	2.5	-4.0	0.9	13.2	6.2	3.7	13.9	8.8	3.3		
Treeline	4120	-10.9	1.36	-5.14	-0.2	12.1	5.1	2.7	12.9	7.8	2.2		
<i>Abies spectabilis</i> , WET/Kathmandu	1336	2.2	18.7	10.5	15.7	28.6	22.2	20.2	28.2	24.2	18.6	1466	943
Forest line	3770	-12.4	4.1	-4.1	2.1	14.9	8.6	7.5	15.5	11.5	4.7		
Treeline	3910	-13.2	3.3	-4.9	1.3*	14.2	7.8	6.8	14.8	10.8	3.9		

*Absolute minimum sometimes goes below 0°C

564 **Table 4.** Pearson correlation coefficients (*r*) between daily minimum, maximum and mean temperature recorded by temperature loggers installed
565 at the forest line locations at 2 m height above ground, of the study sites (DRY and WET) and data available from lower elevation climate
566 stations (Chame, Kathmandu). Correlation coefficients are calculated independently for two years. All values are significant at $p < 0.0001$.
567

Year	Logger at DRY vs. Station at Chame			Logger at WET vs. Station at Kathmandu		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
2010	0.86	0.88	0.90	0.95	0.77	0.95
2011	0.91	0.87	0.91	0.94	0.73	0.94

Draft

Table 5. Pearson correlation coefficients (r) among the four residual tree-ring chronologies from the two study sites, DRY and WET, for the analytical windows 1978–2007. Values are Pearson’s product-moment correlation coefficients. FL = forest line elevation, TL = treeline elevation. *** indicates $p < 0.001$.

	FL-DRY	TL-DRY	FL-WET	TL-WET
<u>1978-2007</u>				
FL-DRY	1	0.27	0.05	0
TL-DRY		1	0.01	0.02
FL-WET			1	0.41*
TL-WET				1
<u>1968-1996</u> [▪]				
Ngawal BS	0.72***	0.30	-	-
Pisang BS	0.59***	0.30	-	-

[▪] Chronologies from the forests in Ngawal and Pisang located near DRY and used by Cook et al. (2003); were made available by Paul J Krusic. ‘BS’ is named after Dr. Berghart Schmidt.

577 **Table 6.** Pearson correlation coefficients (*r*) of monthly climate-growth relationships at two elevations of the two study sites by the moving
578 window method over the available common period (1978-2007). * indicates *p* < 0.05; ** indicates *p* < 0.01.

Pinus wallichiana, DRY										Abies spectabilis, WET										
Forest line						Treeline					Forest line					Treeline				
Temperature																				
September _{t-1}	0.60**	0.56*	0.54*	0.41	0.61**	0.02	0.05	0.05	0.11	0.11	-0.25	-0.18	-0.05	0.15	0.13	-0.65**	-0.62**	-0.51*	-0.21	0.17
October _{t-1}	0.02	0.02	-0.03	-0.09	-0.12	0.15	0.13	-0.12	-0.10	-0.06	-0.57**	-0.55*	-0.37	-0.30	-0.41	-0.20	-0.10	0.04	0.02	0.12
November _{t-1}	-0.23	-0.25	-0.30	-0.37	-0.39	0.33	0.33	-0.31	-0.30	-0.23	0.09	-0.04	0.17	-0.03	-0.05	0.03	-0.19	-0.01	0.03	0.18
December _{t-1}	0.03	0.10	0.06	0.14	-0.02	0.07	0.07	0.06	-0.11	0.09	-0.14	-0.21	-0.10	-0.34	-0.35	0.12	0.02	0.18	0.07	0.18
January _t	-0.06	-0.17	-0.19	-0.38	-0.61**	0.13	0.04	0.02	-0.09	0.08	-0.07	-0.01	0.04	-0.23	-0.12	-0.09	-0.01	0.05	-0.11	0.12
February _t	0.08	-0.15	-0.21	-0.14	-0.24	0.05	0.17	-0.08	-0.01	-0.01	-0.05	0.01	0.18	0.11	0.22	-0.15	-0.13	0.07	0.12	0.30
March _t	0.18	0.21	0.17	0.06	-0.04	0.36	0.33	0.34	0.39	0.36	-0.40	-0.30	-0.13	0.17	0.15	-0.13	0.01	0.23	0.39	0.46*
April _t	0.25	0.17	0.12	-0.01	-0.13	0.05	0.06	-0.09	-0.02	0.06	-0.30	0.46*	-0.26	-0.18	-0.13	0.01	-0.16	0.08	0.12	0.31
May _t	0.45*	0.43	0.41	0.29	0.28	0.14	0.21	0.20	0.22	0.25	-0.20	-0.20	-0.21	-0.30	-0.33	-0.21	-0.30	-0.25	-0.19	0.11
June _t	0.04	0.16	0.21	0.38	0.31	0.04	0.04	-0.14	-0.17	-0.21	-0.30	-0.30	-0.19	0.01	0.10	-0.54*	-0.64**	-0.61**	-0.43	-0.12
July _t	-0.16	-0.11	-0.10	0.00	0.07	0.05	0.08	-0.09	-0.18	-0.23	0.41	0.32	0.39	0.38	0.43	0.24	0.07	0.07	0.29	0.50*
August _t	-0.30	0.00	-0.02	-0.06	-0.04	0.29	0.32	-0.30	-0.26	-0.18	-0.20	-0.20	-0.04	0.33	0.40	-0.07	-0.12	-0.04	0.23	0.50*
Precipitation																				
September _{t-1}	-0.01	0.01	-0.07	-0.14	-0.27	0.01	0.03	-0.03	0.03	0.10	-0.53*	-0.48*	-0.53*	-0.30	-0.22	0.08	0.26	0.17	0.36	0.24
October _{t-1}	0.03	0.15	0.29	0.37	0.42	0.23	0.15	0.00	-0.03	-0.08	-0.15	-0.23	-0.26	-0.15	0.02	0.09	0.01	0.02	0.22	0.22
November _{t-1}	0.02	-0.04	0.00	0.34	0.38	0.08	0.15	0.13	-0.02	-0.20	0.22	0.28	0.30	0.32	0.21	0.16	0.30	0.29	0.33	0.17
December _{t-1}	0.32	0.38	0.47*	0.36	0.44	0.01	0.08	-0.18	-0.14	-0.23	0.09	-0.04	-0.10	-0.21	-0.08	-0.21	-0.44	-0.42	-0.45*	-0.48*
January _t	-0.45*	-0.50*	-0.58**	-0.55*	-0.46*	0.11	0.13	0.13	0.13	0.13	0.01	0.12	0.17	0.33	0.18	-0.05	0.12	0.15	0.30	0.09
February _t	-0.32	-0.29	-0.25	-0.08	0.04	0.35	0.35	-0.48*	-0.53*	-0.59**	-0.02	0.08	0.35	0.19	0.29	-0.25	-0.18	0.20	0.12	0.28
March _t	-0.23	-0.16	0.01	0.16	0.25	0.19	0.16	-0.28	-0.28	-0.33	0.40	0.34	0.52*	0.48*	0.44	0.00	-0.18	0.07	0.10	0.07
April _t	0.52*	0.50*	0.45*	0.32	0.36	0.11	0.15	-0.07	-0.03	-0.18	0.37	0.49*	0.46*	0.41	0.49*	-0.18	-0.11	-0.15	0.03	0.18
May _t	0.33	0.29	0.28	0.22	0.26	0.07	0.09	-0.08	-0.11	-0.27	0.21	0.13	0.08	-0.04	-0.12	-0.25	-0.49*	-0.51*	-0.57*	-0.49*
June	0.02	0.03	-0.14	0.32	0.31	0.15	0.31	-0.19	-0.23	-0.20	-0.07	-0.13	-0.14	-0.29	-0.39	0.03	-0.04	0.03	0.01	-0.06
July _t	0.46	0.43	0.30	-0.02	-0.24	0.29	0.13	0.14	0.18	0.34	-0.14	-0.03	0.24	0.10	0.08	-0.11	-0.01	0.18	0.03	-0.17
August _t	0.36	0.29	0.22	-0.03	-0.42	0.02	0.16	-0.12	-0.01	0.24	-0.13	-0.02	0.12	0.13	-0.08	-0.14	-0.02	0.07	-0.13	-0.28
	1980-1999	1982-2001	1984-2003	1986-2005	1988-2007	1980-1999	1982-2001	1984-2003	1986-2005	1988-2007	1980-1999	1982-2001	1984-2003	1986-2005	1988-2007	1980-1999	1982-2001	1984-2003	1986-2005	1988-2007

Tree growth response to climatic variability

Figure captions

Fig. 1. Location of the study sites Ngawal (*Pinus wallichiana*, DRY), and Lauribinayak (*Abies spectabilis*, WET) in the Manang and Rasuwa districts, respectively, in central Himalaya, Nepal. ▲ indicates sampling sites and ● indicates climate stations.

Fig. 2. Climate characteristics for climate stations representing study sites. (a-b) Monthly average temperature and precipitation; (c-d) seasonal and annual temperature means; (e-f) seasonal and annual precipitation total; (g) correlation between monthly precipitation data at the Kathmandu and Dhunche stations (line), and between monthly temperature station data from Kathmandu and logger data from the forest line at WET (dark grey bars indicate significant correlation at $p < 0.05$). AMT = Annual Mean Temperature and TAR = Total Annual Rainfall. * indicates $p < 0.05$; ** $p < 0.01$, and *** $p < 0.001$. All data refer to the 1978-2007 period except temperature correlation in panel (g) which is based on the 2008-2011 period.

Fig. 3. Residual chronologies for forest line and treeline elevations at DRY and WET sites for the period 1978-2007.

Fig. 4. Climate–growth relationship shown as radial growth correlation with temperature (upper panels) and precipitation (lower panels) for September_{*t-1*} to August_{*t*}, at forest line and treeline elevations of the DRY and WET sites for the full study period 1978 to 2007. Black bars represent statistically significant correlations where * indicates $p < 0.05$; ** $p < 0.01$.

Tree growth response to climatic variability

Fig. 1.

Tree growth response to climatic variability

Fig. 2.

Tree growth response to climatic variability

611 **Fig. 3.**

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Tree growth response to climatic variability

614 **Figure 4.**

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