Dendrochronologia 41 (2017) 34–43

Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro

Gradual expansion of moisture sensitive *Abies spectabilis* forest in the Trans-Himalayan zone of central Nepal associated with climate change[☆]

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ARTICLE INFO

Article history:
Received 28 August 2015
Received in revised form 15 January 2016
Accepted 31 January 2016
Available online 4 February 2016

Keywords:
Trans-Himalaya
Treeline
Recruitment
Ecotone

ABSTRACT

Population structure and tree recruitment dynamics in the natural treeline ecotone of high mountains are strong indicators of vegetation responses to climate. Here, we examined recruitment dynamics of *Abies spectabilis* across the treeline ecotone (3439–3638 m asl) of Chimang Lekh of Annapurna Conservation Area in the Trans-Himalayan zone of central Nepal. Dendrochronological techniques were used to establish stand age structure by ring counts of adults, and by terminal bud scar count for seedlings and saplings. The results showed abundant seedling recruitment, higher regenerative inertia and colonization with a consistent range shift of the *A. spectabilis* treeline. The upward expansion of this sub-alpine treeline was found to be driven by a strong dependence of seedling recruitment and radial growth on snowmelt and precipitation as temperatures rise. The radial growth of *A. spectabilis* at the alpine timberline ecotone (ATE) and closed timberline forest (CTF) showed sensitivity to spring season (March–May) climate. Tree ring indices of CTF showed a strong positive correlation with spring and annual precipitation, and a significant negative correlation with spring and annual temperature, however, moisture sensitivity was less strong at ATE than CTF.

1. Introduction

The high elevation treeline ecotone forms the transition from the timberline to treeless alpine vegetation (Körner, 2003). Natural treelines are sensitive to climate and are valuable indicators of vegetation responses to climatic change (Kullman, 2002; Körner and Paulsen, 2004; Batllori and Gutiérrez, 2008). Understanding the environmental factors responsible for determining the geographical and ecological limits of species across the globe is important given anthropogenic climate change and its potential effect in natural ecosystems (Summers et al., 2012). Upward shifts of high elevation treelines are generally reported in response to global warming (Kullman, 2001; Grace et al., 2002; Holtmeier and Broll, 2007; Harsch et al., 2009). A recent meta-analysis of worldwide treelines indicated about 52% of global treelines were advancing, 1% of them were retreating and the remaining had no evidence of change (Harsch et al., 2009). Temperature is commonly held to be the main abiotic factor to delimit the position of alpine treelines, and to constrain the growth and regeneration of tree species (Körner, 2003,2012; Holtmeier and Broll, 2007; Jump et al., 2007; Harsch et al., 2009). Hence, as global temperatures rise, treelines are forecast to advance. However, in some climatic conditions, treeline expansion is likely to be limited by insufficient photosynthesis mainly brought about by drought stress (Lloyd and Fastie, 2002; Wilmking et al., 2004; Wang et al., 2015). Therefore, it is important to identify environmental factors associated with treeline formation in order to better understand and predict treeline response to changing climate.

Air temperatures across most mountainous regions of the world are expected to rise significantly over coming decades (IPCC, 2013). However, the response of treelines to warming is still subject to great uncertainties on how local factors (e.g., elevation, expo-

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[☆] This article is part of a special issue entitled "Asian Dendrochronology Association (ADA) 2015", published in the journal Dendrochronologia 41, 2017.

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http://dx.doi.org/10.1016/j.dendro.2016.01.006

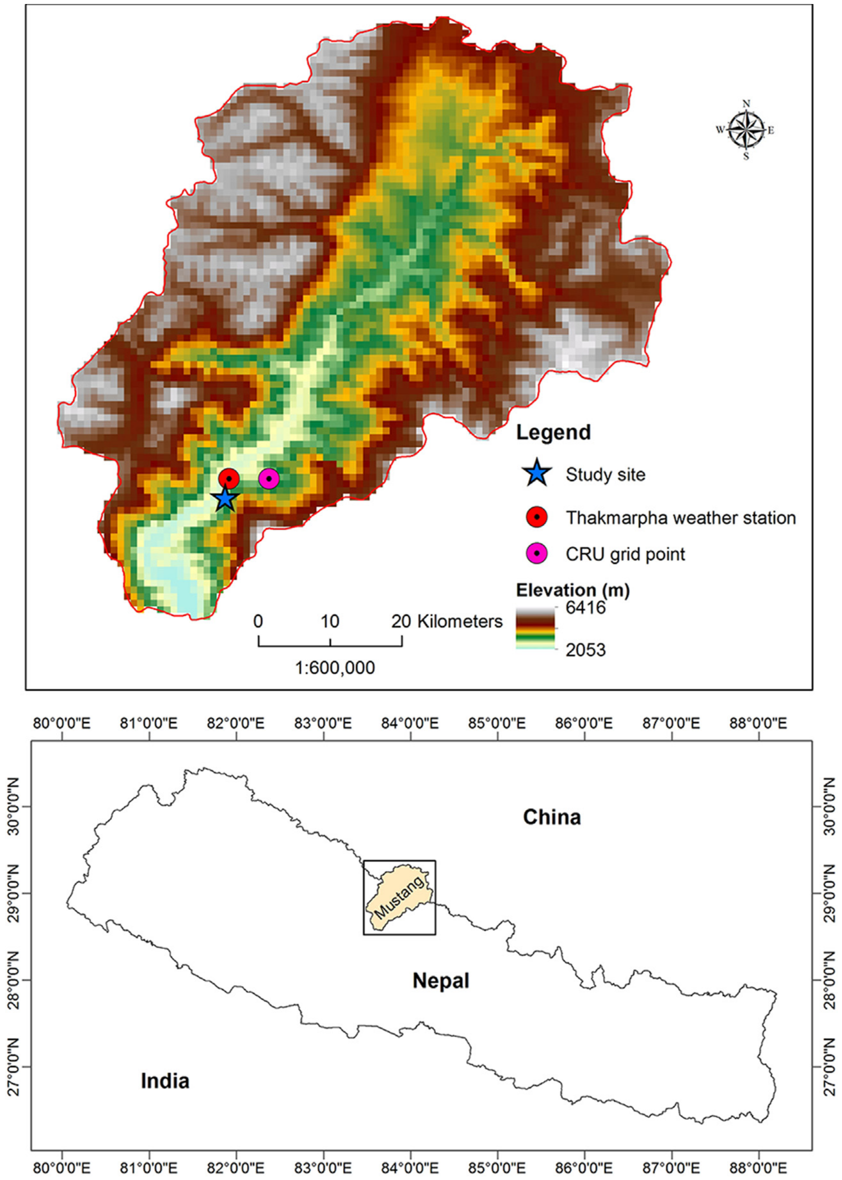

Fig. 1. Map of Nepal showing Mustang and study sites at Chimang (Chimang I and Chimang II transects), Thakmarpha climate station and CRU grid point.

sure, aspect, soil) will modulate treeline dynamics (Greenwood et al., 2014). Seedling recruitment and colonization, stand densification and regenerative inertia of the treeline can vary greatly between slope aspects due to the differential presence of permafrost (Danby and Hik, 2007), and factors such as stand history, dispersal ability, habitat suitability, disturbance and ecological interactions (Schloss et al., 2012). Climate induced shifting of alpine treeline is a widespread phenomenon in various mountain systems of Northern hemisphere (Gaire et al., 2014; Hagedorn et al., 2014; Qi et al., 2015). However, the Himalayan treeline environment is very heterogeneous, which limits broad generalization on treeline sensitivity to climate due to variation in physiographic configuration and strong climatic gradients (Daniels and Veblen, 2004; Elliott and Kipfmueller, 2011; Schickhoff et al., 2015). Himalayan treelines show different response to recent climate change including substantial upward shifting (Gaire et al., 2014), moderate expansion (Chhetri and Cairns, 2015), almost stationary position (Gaire et al., 2011; Shrestha et al., 2014) and even the possibility of retreating in case of warming induced drought stress (Liang et al., 2014). The overall Himalayan region has sparse information on treeline dynamics, and particularly little is known about the recruitment dynamics of treeline in the Trans-Himalayan dry zones of central Nepal.

The Himalaya has already experienced a relatively high rate of warming with greater magnitude during winter time (Shrestha et al., 2012). The warming episodes are even more intense in the high mountain range and cold deserts of the Trans-Himalayan region, making it most vulnerable of all ecosystems (Xu et al., 2009; Sharma and Tsering, 2009; Aryal et al., 2012). High elevation treeline in the Trans-Himalayan region (Mustang: central Himalaya) is expected to be particularly sensitive to changes in climate as it receives low precipitation and consequently relies on runoff from snow cover as the main source of water (Aryal et al., 2012). This region, therefore, provides a unique opportunity to study the climate response of vegetation in this water-limited high altitude environment.

Here we use inventory data and tree ring records to study the recruitment dynamics and climate response of the *A. spectabilis* treeline in the Trans-Himalayan region. Specifically, we aim to (1) assess spatiotemporal recruitment dynamics of *A. spectabilis* trees

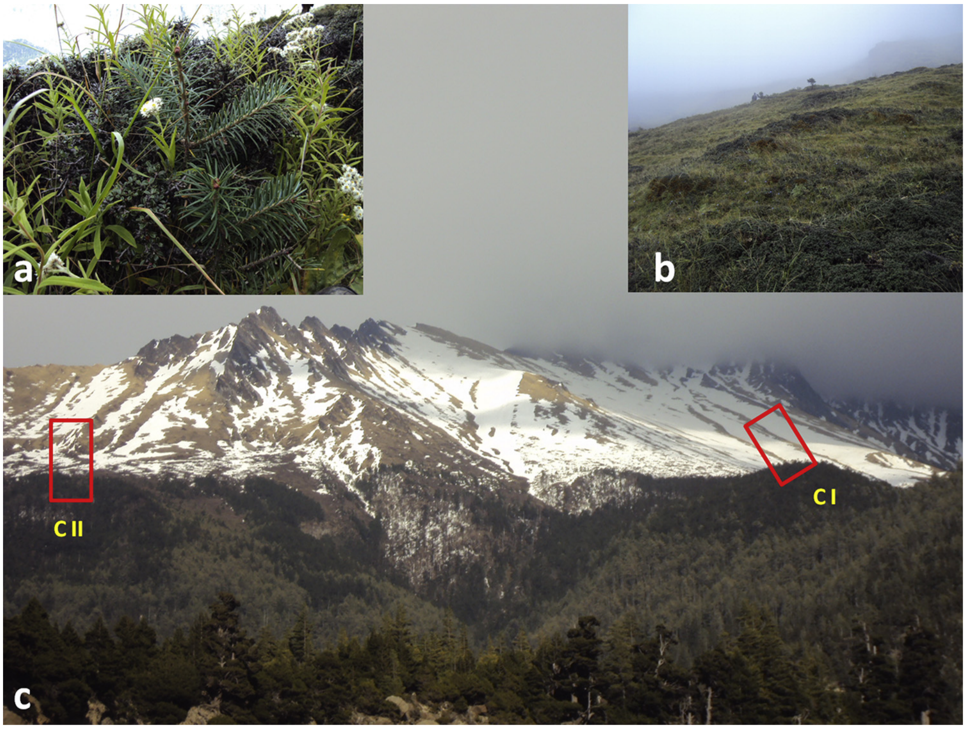

Fig. 2. *Abies spectabilis* seedling under *Rhododendron* bush (a), *A. spectabilis* sapling at the upper limit in Chimang I transect (b), photo showing study transects (transect I and II) at Chimang (CI and CII).

Table 1
Summary statistics of tree structural attributes.

Site	Growth form	Ht (m)	BD (cm)	Age (year)	CC (m^2)	VGR (cm/year)	RGR (cm/year)
CI	Seedling ($n = 36$)	0.32 ± 0.08	1.92 ± 0.58	12.08 ± 4.03	0.65 ± 1.10	2.75 ± 0.59	0.16 ± 0.05
	Sapling ($n = 49$)	0.91 ± 0.42	3.71 ± 1.56	20.53 ± 6.00	0.97 ± 0.78	4.56 ± 1.90	0.18 ± 0.08
	Tree ($n = 55$)	6.36 ± 3.71	19.53 ± 10.34	41.10 ± 17.30	6.06 ± 3.14	15.19 ± 5.08	0.46 ± 0.14
CII	Seedling ($n = 18$)	0.38 ± 0.06	2 ± 0.30	12.70 ± 2.20	1.35 ± 0.95	3.18 ± 0.63	0.16 ± 0.03
	Sapling ($n = 28$)	1.06 ± 0.37	5.94 ± 3.48	19.44 ± 7.08	1.07 ± 0.93	5.58 ± 1.71	0.31 ± 0.18
	Tree ($n = 52$)	8.66 ± 5.43	18.64 ± 10.43	36.69 ± 12.25	7.35 ± 4.35	22.64 ± 10.41	0.49 ± 0.18

(Ht, Height; BD, Basal Diameter CC, Canopy Cover; VGR, Vertical Growth Rate; RGR, Radial Growth Rate; *n*, Number of Individuals; the first number represents mean value and the second number represents the standard deviation for each column).

at the treeline ecotone and (2) determine the climate response of plant growth and regeneration underlying observed changes.

2. Materials and method

2.1. Study area

The study was carried out at Chimang Lekh in the southern part of south–west facing slope of Mustang District (Fig. 1) in the Trans-Himalayan zone of central Nepal. While politically in Nepal, geographically the region of Mustang is a part of Tibetan Highlands (Stainton, 1972) with most of the land in a rain shadow receiving less than 200 mm annual rainfall. Particularly, the northern part of the district lies in the Trans-Himalayan region with semi-arid and dry climate; hence forested area is confined to the southern part of district covering only 12,324 ha (3.24%) of its total landmass (Government of Nepal, 2010). The study area lies within the Annapurna Conservation Area (ACA) which harbors prime habitat for diverse flora and fauna (Bhattarai et al., 2010; Government of Nepal, 2010; Aryal et al., 2012).

The arid zone alpine flora of the Trans-Himalayan range is closely related to that of eastern Tibet and western China (Shrestha et al., 2005). Most of the vegetation is composed of scarce and scattered patches of thorny cushion plants such as *Caragana*, *Astragalus*, and *Lonicera* species while ravines and riverbanks are dominated by species from the genera *Hippophae, Myricaria, Populus* and *Salix*. *Abies spectabilis* occurs predominantly in more sheltered areas and usually grows under moist climatic conditions in sub-alpine Himalayan forests (3000–4000 m asl) and occasionally extending its upper limit to 4300 m asl. This species is characterized by low branching, dense foliage and is usually associated with *Betula utilis* and *Rhododendron campanulatum* at the upper limit (Yadav et al., 2004). Notably, *A. spectabilis* forest in the study area is found at comparatively low elevation (2800–3638 m asl) associated with *Pinus wallichiana*.

2.2. Field sampling

Field investigations were carried out during September of 2014. Sampling was conducted in two elevation transects on a topographically uniform area of sub alpine treeline ecotone. The ecotone includes the uppermost distribution limit (species limit) of *A. spectabilis* (irrespective of age) and the uppermost timberline. We have considered the treeline as the uppermost elevation of trees ($\geq$2 m) and timberline as the uppermost closed forest with tree density (trees >5 m tall) of at least 30% coverage (Holtmeier, 2003). The first transect Chimang I (hereafter CI) was 20 m × 130 m, and the second transect Chimang II (hereafter CII) was 20 m × 180 m (Fig. 2).

Table 2
Summary statistics of ecotone attributes.

Ecological parameters	Chimang I	Chimang II
Total individuals recorded (living and dead)	161	129
Total individuals mapped	140	98
Density of living individuals (hectare^{-1})	77.40	44.79
Density of dead individuals (hectare^{-1})	3.84	5.55
Seedling sapling ratio	0.52	0.41
Occurrence of fire scar in tree cores	13%	17%
Max. range of range shift of tree limit (m year^{-1})	0.52	1.74
Mean rate of treeline shift (m year^{-1})	0.50	2.21

The longer axis of each plot was parallel to the altitudinal gradient of subalpine forest to alpine shrub land. The altitudes of lower and upper parts of the plots were recorded by GPS. We located all the individuals of *A. spectabilis* within transects and classified them into three-height classes: trees (≥2 m), saplings (0.5–2 m) and seedlings (<0.5 m) (Wang et al., 2006; Kullman, 2007). Basal diameter (BD: <10 cm from base), tree height and the canopy crown were measured.

Dendrochronological techniques were employed for age estimation and radial growth measurement of trees within alpine timberline ecotone (ATE) transects and closed timberline forest (CTF). All ATE trees with basal diameter (BD) >5 cm were cored at the base of the tree (<30 cm), whereas tree cores were collected from breast height level at CTF, using an increment borer. We estimated tree age based on the number of annual rings at the base. In case of trees with missed pith, the number of missing rings was determined by the geometric method (Duncan, 1989). The ages of saplings and seedlings (height < 2.5 m and DBH ≤ 5 cm) were estimated non-destructively in the field by counting terminal bud scars (internodes or branch whorls) along the main stem (Camarero and Gutiérrez, 2004; Wang et al., 2006). Tree cores were air dried and mounted on sample holders and the wood surfaces were sanded using progressively finer sandpaper according to standard methods (Fritts, 1976). Ring widths were measured at a resolution of 0.01 mm with a LINTAB II measuring system (Rinntech, Germany).

2.3. Demographic structure

We calculated average population density of *A. spectabilis* per hectare for each transect. The density diameter relationship was calculated between densities of individuals per hectare with basal diameter to assess regeneration status. The population density of individuals was compared with tree recruitment patterns at every five-year interval, and seedling sapling ratio was calculated. Pearson correlation analyses were performed to evaluate association between variables: the relationship between age, height, basal diameter and crown coverage of individuals within transects. We calculated mean annual radial and vertical growth by dividing an individual's radius and height with the age of the individual. Statistical analyses were performed using the software R (version 2.8.1, R Development Core Team, 2008).

2.4. Treeline dynamics

Treeline advance was estimated by subtracting the elevation of the position of old adult trees (down slope) from the present treeline position (upslope), following Gamache and Payette (2005). This gave the approximate recent upward shift of the treeline; the total shift was divided by the age difference between upslope and downslope tree individuals to estimate the rate of shift per year. This rate of shifting was calculated with each uppermost and younger trees from the oldest tree of lower elevation within transect in order to homogenize the rate of multiple trees across the ecotone.

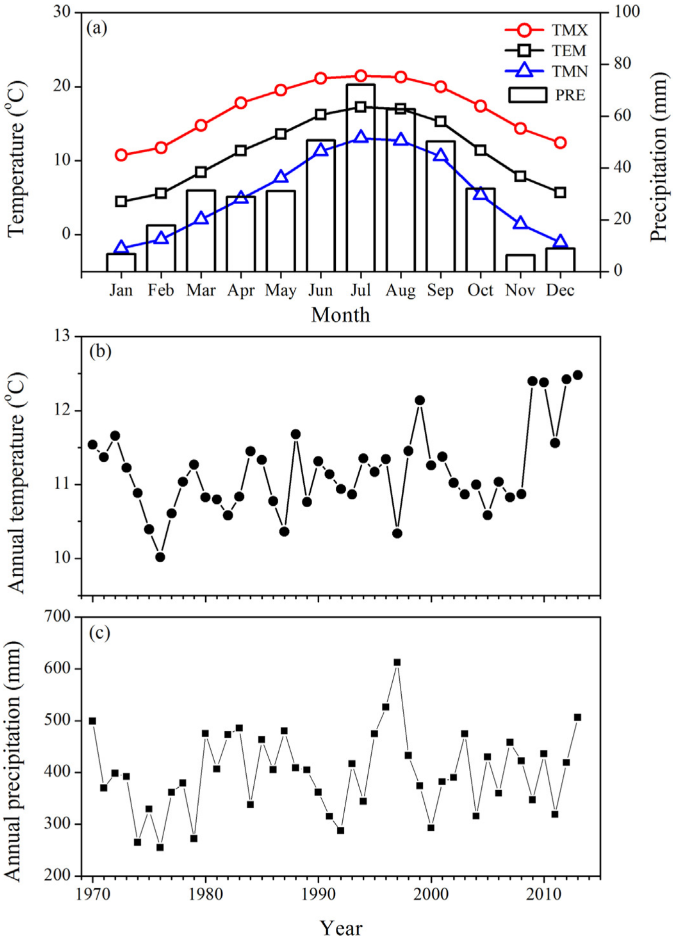

Fig. 3. Climate summary of Thakmarpha (1970–2013 AD); monthly maximum temperature (TMX), monthly mean temperature (TEM), monthly minimum temperature (TMN) and monthly precipitation (a), annual temperature trend (b), and Annual precipitation trend (c).

2.5. Climate growth response

Climatic data were collected for the period 1970–2013 from the nearest meteorological station (Thakmarpha: 28°45′ N, 83°42′ E, 2566 m asl), located at about 4 km apart from study sites (Fig. 1). Mean annual rainfall in the area is 393 mm with mean annual temperature 16 °C. The climate summary is presented in Fig. 3. The treeline ecotone is generally covered by snow for in excess of four months from mid of November to mid of March (personal observation).

Tree cores were cross-dated by visual inspection (Stokes and Smiley, 1968) and by statistical tests (sign-test and *t*-test) using the software package TSAP-Win (Rinn, 2003). Tree cores having low correlation with the master chronology ($r < 0.5$) and those having fire scars were excluded from further analysis. We combined the treeline chronologies of *A. spectabilis* from CI and CII to form a composite ATE chronolgy, while doing so we checked the correlation between individual site chronologies (0.239, $n = 45$). Ring-width measurements were detrended with a negative exponential or a linear regression function, with the help of ARSTAN software (Cook, 1985). Before detrending, a data adaptive power transformation was applied to reduce heteroscedastic behavior of tree-ring series (Cook and Peters, 1997). Tree-ring indices were calculated as the differences between transformed ring-width measurements and fitted curves. The common signal among individual tree-ring series was maximized by the detrending method, while low frequency trends due to tree aging and stand dynamics were removed. All

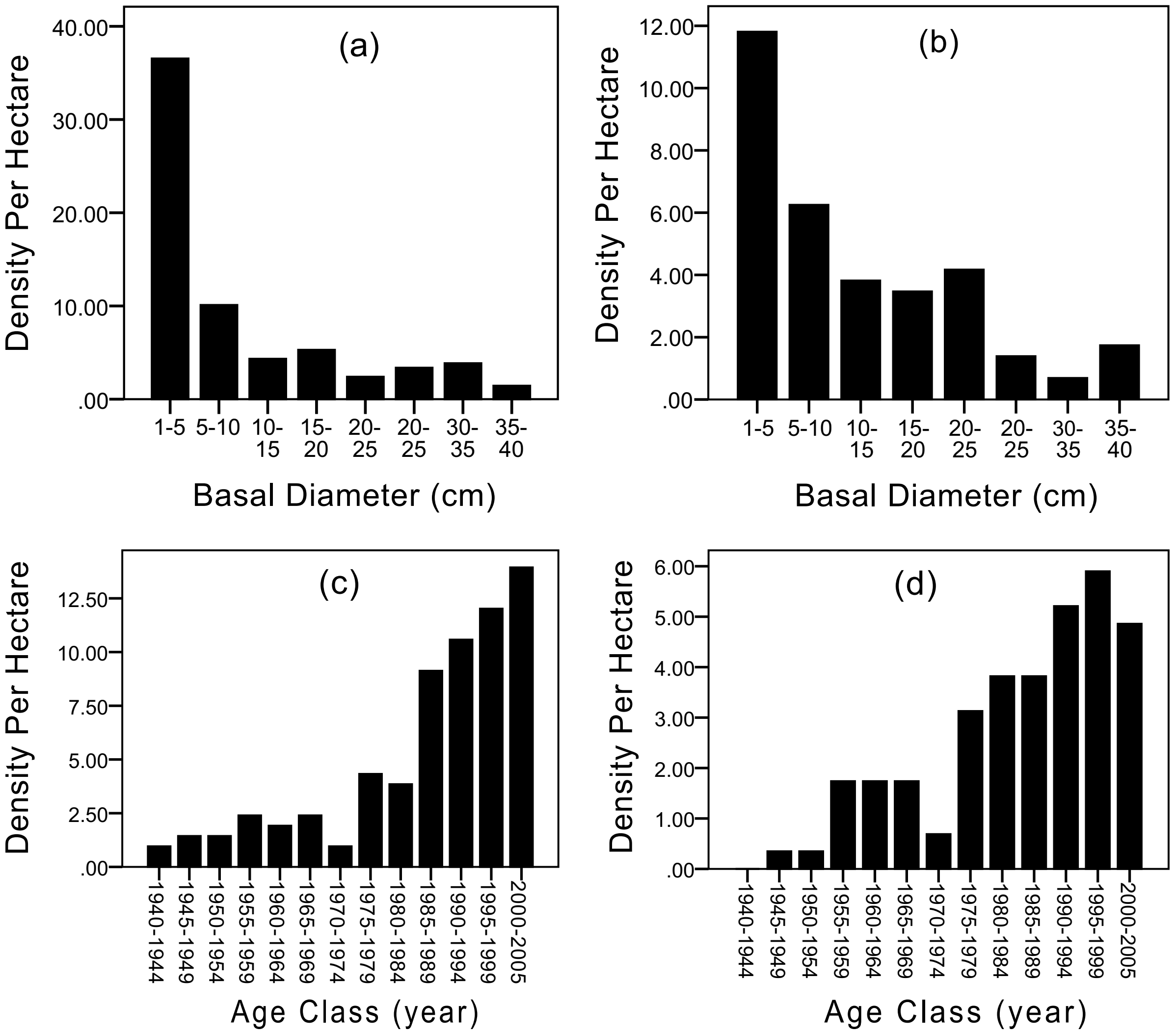

Fig. 4. Density (per hectare) and basal diameter in transect CI (a) and transect CII (b), density (per hectare) and age class of individuals showing recruitment trend in transect CI (c) and transect CII (d).

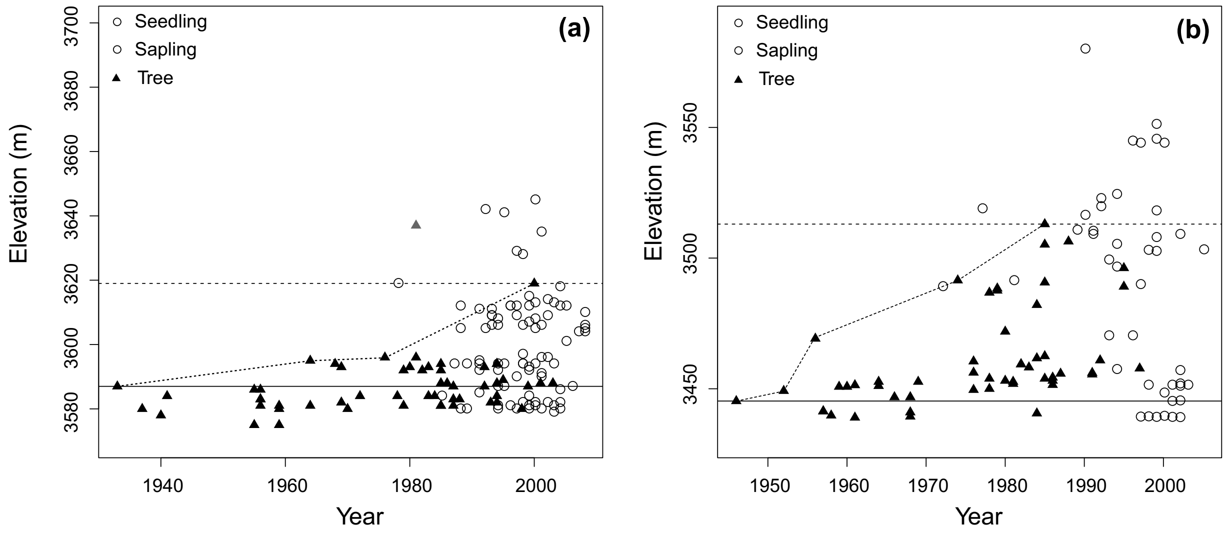

Fig. 5. Range shift of treeline and spatiotemporal distribution of tree recruitment across treeline at CI (a) and CII (b) transects. The upper dotted line in the figures represent the recent position of treeline and the solid line below shows the position of oldest tree in the transects, (the uppermost treeline in at CI was considered after excluding the single isolated tree at the uppermost elevation (a).

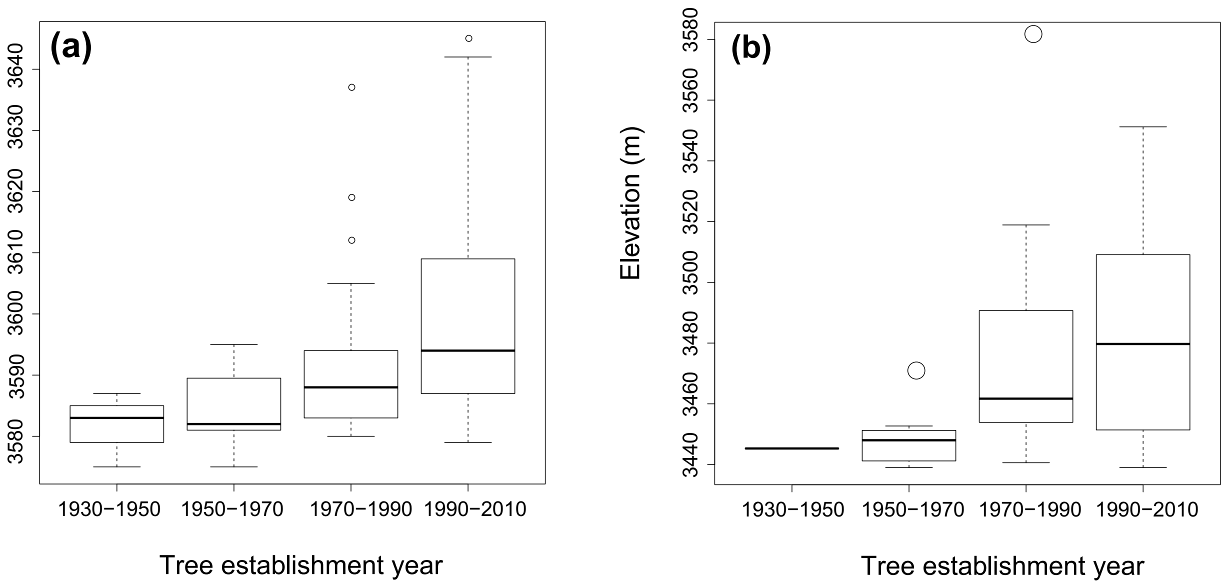

Fig. 6. Decadal variation of tree establishment periods in elevation of the transect at CI (a) and CII (b).

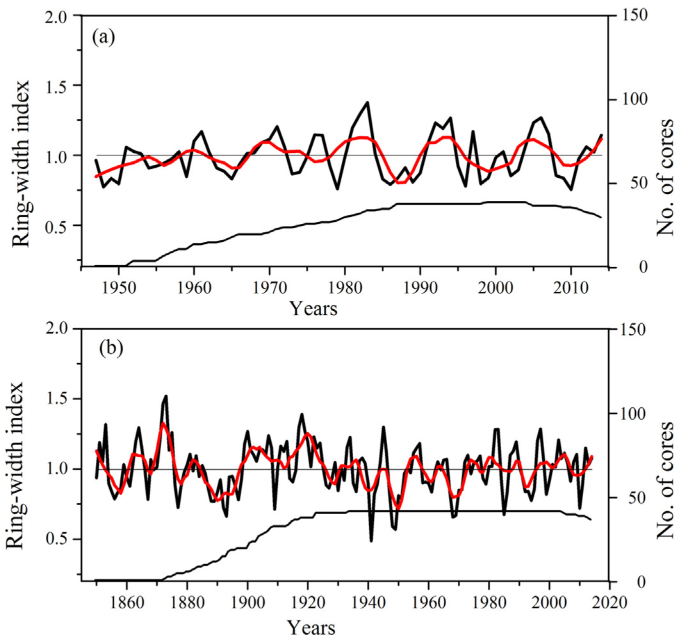

Fig. 7. Tree ring standard chronology of *Abies spectabilis* from Chimang (Mustang, central Nepal): ATE (a), CTF (b).

detrended series were averaged to chronologies by computing the biweight robust mean in order to reduce the influence of outliers (Cook and Kairiukstis, 1990). Variance stabilization (Osborn et al., 1997) was applied to adjust for changes in variance associated with declining sample size (number of trees) over time. Descriptive statistics were calculated for the standardized chronologies. The variability of measurements for the whole series was estimated through standard deviation (SD), autocorrelation, and mean series correlation. The quality of site chronology was indicated by signal-to-noise ratio and expressed population signal (EPS). A level of 0.85 for EPS was considered to indicate a satisfactory quality of a chronology (Wigley et al., 1984).

Climate in the preceding growing season has a strong influence to tree growth in the following year (Fritts, 1976). As dendrochronological studies and field observation revealed, radial growth of *A. spectabilis* at treeline sites almost ceases in September–October (Sano et al., 2005). Growth-climate relationships were accessed by correlating site standard chronology with climatic variables (precipitation, mean/maximum/minimum air temperature), from June of the previous growth year until October of the current growth year.

3. Results

3.1. Stand age structure and demography

We surveyed a total of 238 individuals of *A. spectabilis* including trees, saplings and seedlings (>20 cm tall). Small seedlings (<20 cm tall) were only included in density calculations (Table 1). The density of individuals was 77.4 ha^{-1} at CI and 44.9 ha^{-1} at CII (Table 2). Age and basal diameter measurements revealed that individuals at CI were older (<80 years) than CII (<67 years). We observed a similar recruitment pattern in both transects: the largest number of individuals was of 10–30 years of age and most of the individuals established during the year (1990–2000 AD). Comparatively fewer seedlings and saplings were established above the treeline. Tree establishment was not continuous over time, with a gap during the periods between 1970 and 1974. The proportion of young trees (<50 years old) of *A. spectabilis* was high at both sites; 86% at CI and 89% at CII. There were 8 and 16 dead individuals in transects CI and CII respectively (Table 1). The density–basal diameter distribution followed a reverse 'J-shaped' pattern and showed the higher regenerative inertia in both transects (Fig. 4). It was observed that the juveniles preferentially established in the recent decades and the recruitment was higher around treeline.

3.2. Treeline dynamics

The species limit of *A. spectabilis* was recorded at 3645 m asl (CI) and 3580 m asl (CII). The treelines (representing the uppermost position of 2 m tall trees) were located at 3619 m asl at CI and 3513 m asl at CII, which were established during 1978 (CI) and 1985 (CII). The uppermost individual occurred 8 m and 57 m above treeline at CI and CII respectively (Fig. 5a,b). The box plots showed the maximum recruitment occurred at the highest elevation in both CI and CII (Fig. 6). On the basis of tree establishment date, the maxi-

Table 3
Tree-ring chronology summary statistics.

Sampled location *A. spectabilis*	Elevation Range (m asl)	Chronology length (years)	No of trees (cores)	Mean sensitivity	EPS	Series intercorrelation	1st order autocorrelation
Alpine treeline ecotone (ATE)	3439–3638	68	36 (40)	0.326	0.931	0.472	0.612
Closed timberline forest (CTF)	3000–3300	165	24 (42)	0.2	0.946	0.597	0.615

mum range of treeline shift was quantified as 0.52 m year^{-1} at CI and 1.74 m year^{-1} at CII (Table 2).

3.3. Climate growth response

We produced standard tree ring-width chronolgies of 68 years using 40 tree cores from 36 trees at ATE (3439–3638 m asl), and of 165 years using 42 tree cores from 24 trees at CTF (3000–3300 m asl) (Fig. 7a,b). The chronology statistics are presented in Table 3. Both ATE and CTF chronologies revealed that there was no constant increment or decrease in tree radial growth but it fluctuated through times. The ATE radial growth of *A. spectabilis* showed higher correlation with spring season (MAM) climate. The ATE ring width series showed positive correlation with current May ($r = 0.27$, $P < 0.05$) and previous year's June precipitation, but significant negative correlation for maximum ($T_{\max}$, $r = -0.42$, $P < 0.05$) and mean (T_{mean}, $r = -0.46$, $P < 0.05$) temperature for current year April (Fig. 8a,b). This climate growth relation indicated that the treeline is moisture sensitive. The CTF ring-width indices showed significant positive correlation with previous year November ($r = 0.34$, $P < 0.05$), current March–May ($r = 0.52$, $P < 0.05$) and annual precipitation ($r = 0.41$, $P < 0.05$) (Fig. 9b). We found a significant negative correlation between tree-ring indices and spring season maximum ($T_{\max}$, March–May, $r = -0.32$, $P < 0.05$) and mean annual temperature (T_{mean}, $r = -0.32$, $P < 0.05$) (Fig. 9a). The correlation between ring-width series and spring season precipitation was higher at CTF than ATE.

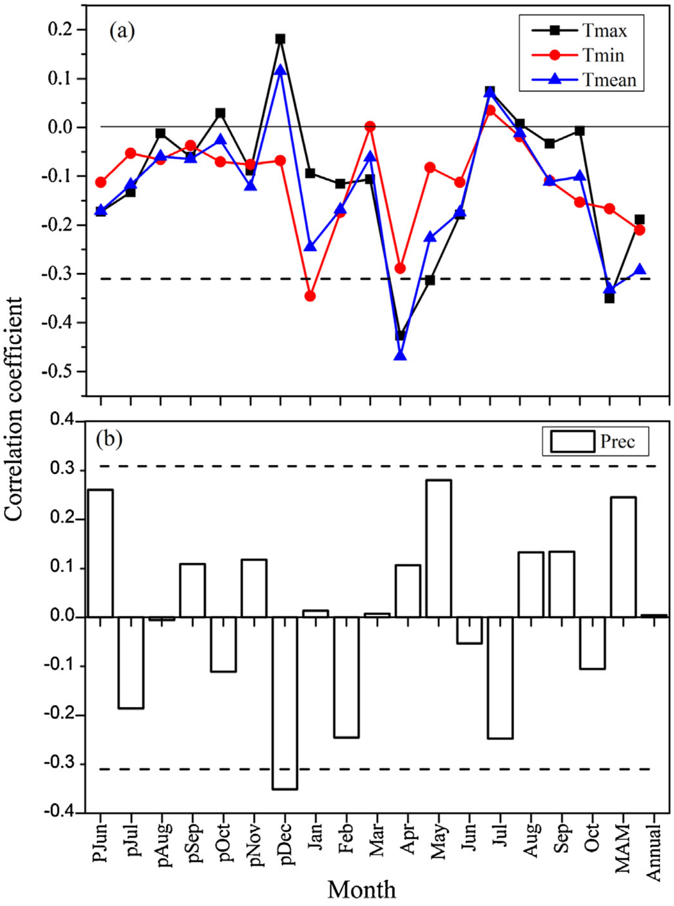

Fig. 8. Relationship between radial growth of *Abies spectabilis* at ATE with climate data: monthly maximum, monthly mean, spring (March–May) and annual temperature, showing (a), monthly, spring (March–May) and annual precipitation (b), both figures show the radial growth response to monthly temperature and precipitation of June in the previous year to October of the current year as well as the spring season and annual climate; dashed horizontal lines indicate significant correlation at 95% confidence limit for a two-tailed test.

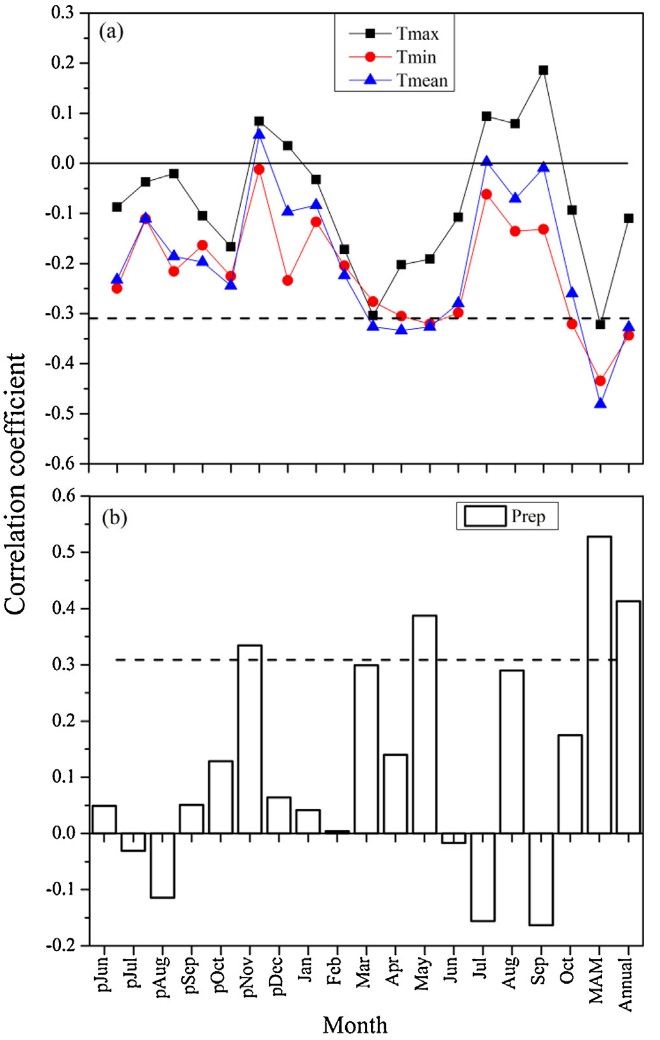

Fig. 9. Relationship between radial growth of *Abies spectabilis* at CTF with climate data: monthly maximum, monthly mean, spring (March–May) and annual temperature, showing (a), monthly, spring (March–May) and annual precipitation (b), both figures show the radial growth response to monthly temperature and precipitation of June in the previous year to October of the current year as well as the spring season and annual climate; dashed horizontal lines indicate significant correlation at 95% confidence limit for a two-tailed test.

4. Discussion

4.1. Stand age structure and demography

Tree recruitment is the critical determinant of movement of the upper forest boundary (Camarero and Gutiérrez, 2007). Our study showed comparatively younger treeline stands indicating that juveniles preferentially established in recent decades (1990–2000 AD) (Fig. 5). The increased recruitment could be attributed to sufficient moisture combined with increased temperature in the region (Cook et al., 2003; Sano et al., 2005; Shrestha et al., 2012), although legacy effects of past climatic changes cannot be fully excluded (Gaire et al., 2014). Increased recruitment and stand densification in recent decades have been reported in various treeline ecotones in Himalaya and Tibet (Batllori and Gutiérrez, 2008; Gaire et al., 2011, 2014; Liang et al., 2011; Lv and Zhang, 2012). The higher size class distribution of younger trees in the ecotone also revealed higher regeneration potential as reported by Lv and Zhang (2012). The considerably denser juvenile population of *A. spectabilis* in the ecotone (more than 85% of individuals <50 years) indicated higher regeneration potential and stand densification in the future. However it is unlikely that all seedlings will survive in the extreme environment of the treeline. The seedling recruitment is more sensitive to climate than adult survival due to lower climatic threshold of juveniles (Lloyd, 1997). The reverse 'J-shaped' density-diameter relationship and high density of seedlings and saplings in the treeline ecotone is the clear indication of sustainable regeneration (Vetaas, 2000). Similar regeneration trends have also been reported from central Himalayan treeline in *A. spectabilis* (Ghimire and Lekhak, 2007) and *B. utilis* (Shrestha et al., 2007).

4.2. *Treeline dynamics*

In the study area, the treeline is found at a relatively low elevation, potentially due to the low precipitation of the region (about 393 mm annual). Here, the treeline is shaped by the unique topographic configuration and climate circulation system in the Trans-Himalayan arid region. With increasing distance from Annapurna massif to the north, the timberline elevation decreases and further to the north, the landscape takes on a Tibetan character, devoid of Trees—a pattern similar to that of the Nanga Parbat massif in NW Himalaya (Schickhoff, 2005).

Himalayan treeline ecotones vary considerably in altitudinal position, physiognomy, species composition, and the high but locally variable anthropogenic pressure on southern aspects disrupts the general pattern (Schickhoff, 2005). However, our findings are in agreement with treeline shift reports in the Himalaya (Dubey et al., 2003; Gaire et al., 2014) with considerable recruitment in the recent decades especially after 1950s as also reported by Liang et al., 2011; Shrestha et al., 2014. We observed a difference in the elevation of the treeline in CI (3637 m asl) and CII (3513 m asl) transects even within a short distance (<5 km) in the same mountain slope potentially since CI is more moist and less exposed whereas CII is drier and fully exposed to south west irradiation and wind direction. We infer that the slope exposure and wind velocity are likely to have shaped the position of treeline, as also identified by Greenwood et al. (2014).

The continental climate regime of the inner Himalayan highlands, including Trans- Himalaya is expected to exert a particularly strong influence of changing climate on treeline dynamics. Our results provide evidence for a moderate rate of treeline movement in recent decades, quantified as 0.52 m year^{-1} at CI and 1.74 m year^{-1} at CII. Both transect showed considerably higher density of saplings near the treeline, and with some saplings even older than neighbouring 2 m tall trees. It is expected that the treeline will continue to advance upward so long as precipitation (both rainfall and snowfall) remains sufficient to maintain growth and establishment as temperatures increase. This pattern is supported by other recent findings of treeline advance linked to rising regional temperatures (Lv and Zhang, 2012; Gaire et al., 2014). Although more or less stationary treeline position (Gaire et al., 2011; Shrestha et al., 2014) as well as moderate shifting (Chhetri and Cairns, 2015) were also reported in central Himalaya, this response is not universal in the region. We have observed a stable precipitation trend (annual and spring), which possibly facilitated increased recruitment during the recent period while the temperature is rapidly increasing in the region. In a similar study, increased winter precipitation was described as the main driving factor of upward shifting of the treeline and tree establishment in the Ural Mountains in Europe (Hagedorn et al., 2014).

While we concentrate on natural treelines, it is critically important to understand the interaction between climate change and altered land use (Vittoz et al., 2008), in order to assess the potential for treeline advance beyond the current climatically determined upper limit. We report prolific regeneration, increased tree establishment and invasion into treeless areas above the forest limit, as directional changes readily attributed to effects of climate change. However in most cases, pastoral abandonment or other human impact also drives treeline dynamics (Holtmeier, 2009; Schickhoff, 2011; Ameztegui et al., 2016). Excessive grazing pressure and widespread fire were reported as the main agents for lowering treelines in Himalaya (Beug and Miehe, 1999), which applies for most anthropogenic treelines in Nepal Himalaya. Along transects, we did not observe any cut stumps and recent fire record in the ecotone showing diminished anthropogenic pressure in recent decades. However a proportion of tree cores (13% in CI and 17% in CII) (Table 1) showed fire scars dated back to 20–30 years indicating the incidence of past fire, although the fire was not recorded in the specific year/years. Evidences of cattle herbivory were found in the ecotone, but there was no evidence of browsing on *A. spectabilis* as it is not palatable for cattle. It showed that changes in grazing pressure were unlikely to influence the treeline shift (Hofgaard, 1997). Notably, our study site was included in Annapurna Conservation Area established in 1992; which considerably controlled forest fire and firewood collection. We consider that decrease in land use pressure and fire frequency is likely to have increased the potential for forest expansion towards higher elevations in conjunction with the climatically driven changes reported above.

4.3. *Climate growth response*

Climate data for the study region showed a significant warming and a stable precipitation trend over recent decades contrary to the enhanced frequency of winter and pre-monsoon drought from western Nepal (Wang et al., 2013). We did not observe a constant increase or decrease in radial growth of *A. spectabilis* at ATE or CTF, contrary to the enhanced radial growth in the recent decades as reported in western Himalayan conifers (Borgaonkar et al., 2011). ATE radial growth showed significant negative correlation with April temperature, and positive correlation with May precipitation indicating that the ATE is sensitive to spring season (March–May) climate. The significant negative correlation of ATE radial growth with minimum January temperature could be associated with snow pack accumulation. Most precipitation falls in the form of snow at this time and higher temperatures will negatively impact accumulated snowpack. Timing, quantity and duration of snow accumulation are highly important factors in the study area since radial growth in the early spring is facilitated by snow melt and early onset of growing season (Vaganov et al., 1999; Bekker, 2005). However after complete melting of snow; the area is rapidly exposed to dry conditions until the summer precipitation, potentially exposing individuals to drought stress. Such drought exposure could affect growth and seedling establishment at treelines, and may even cause treeline retreat in cases of severe drought (Liang et al., 2014). Gaire et al. (2014) reported the *A. spectabilis* treeline in central Nepal to be temperature sensitive and described higher winter temperatures prior to the growing season to be highly correlated with tree growth. Highlighting the potential for variation in early-season conditions to impact *A. spectabilis* growth, Gaire et al. (2014) identified the positive contribution of earlier snow melt to increasing soil moisture for tree growth.

Tree radial growth in CTF showed significant positive correlations with May precipitation and negative correlation with spring temperature (March), indicating that cool and moist spring is conducive for tree radial growth. Here, we reported a similar climate growth response at ATE and CTF, although the strength of the correlation differed (Figs. 8 and 9). Generally warmer springs are expected to be associated with elevated frost damage and lower water availability, with consequent negative impacts on tree growth. Our results showed consistency with other studies carried out in Nepal Himalaya on *A. spectabilis*, which also described ring width to be more sensitive to dry spring (March–May) climate with positive correlation with precipitation and negative correlation with temperature (Cook et al., 2003; Sano et al., 2005; Gaire et al., 2011). Our findings are in agreement with the results of Liang et al. (2014), who have reported a strong positive correlation of total precipitation and negative impact of higher temperature with upper Himalayan treeline on growth of Himalayan birch (*B. utilis*). In apparent contrast, some studies in the Himalayan region found radial growth of *A. spectabilis* to be more sensitive to temperature (Bräuning, 2004; Borgaonkar et al., 2011; Gaire et al., 2014). The authors explained negative correlations between pre monsoon (March–May) climate and radial growth as threshold effects of moisture or temperature, the increased temperature and low precipitation combined with high velocity of wind increases evapotranspiration and causes moisture stress to limit tree growth (Fritts, 1976; Cook et al., 2003; Gaire et al., 2014).

Given the higher regeneration in the recent decades at ATE that we identify, recent increases in temperature are likely to drive increased establishment and tree growth when water availability is not limiting. The improved regeneration of *A. spectabilis* during warm winter and cool summer was also described in relation to past long-term reconstructed climatic data (Cook et al., 2003). Although our results indicated a negative correlation of temperature with radial growth of *A. spectabilis* at ATE, we emphasize that increased temperature still contributes to enhanced recruitment here. Contrary to our findings, Liang et al. (2014) found poor regeneration and lack of recent shifting of *B. utilis* in Nepal Himalaya. They reported increasing moisture stress with a decreasing trend of precipitation coupled with high frequency of missing rings. The higher moisture sensitivity at CTE than ATE could be because of higher temperature and increased competition between trees in comparison to less dense trees at ATE as mentioned by Qi et al. (2015). In a similar study, higher moisture sensitivity below the timberline was also reported by Lv and Zhang (2012).

5. Conclusions

Chimang Lekh of the Trans-Himalayan drier zone of central Nepal is experiencing significant warming and stable annual and spring precipitation trend in recent decades. In this region, *A. spectabilis* showed increased density at the treeline ecotone in recent decades, in conjunction with a gradual increase in elevation. The dry spring climate was found to be critical for limiting plant growth at ATE and CTF. The higher regeneration at the upper forest limit and moderate range expansion of the treeline is likely to be critically dependent on the maintenance of water availability through snowmelt and precipitation as temperature increases. However, further warming and or drier springs could threaten tree growth and recruitment if water availability is critically decreased. The complex topographic configuration and strong climatic gradients across the region make generalising from single treeline studies particularly challenging. Further work across different physiographic regions in the Himalaya is necessary to enable us to scale up such findings, ideally combining recent advances in remote sensing technology with forest inventory ground-truthing plots. It is equally important to distinguish between natural climatic and/or anthropogenic influences on changing plant growth, regeneration and range shifts, to better predict future changes in distribution and improve management of agriculture, horticulture, forest and water resources of the region to cope with the ongoing climatic changes.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgements

We are very grateful to Mr. Raju Bista, KP Sharma, Indra Thakali and Community Forest User Group of Chimang (Mustang) for their contribution to field management and sample collection. The authors would also like to thank Suresh Marahatta, Deepak Kharal, Dr. Krishna Babu Shrestha, Dr. Uttam Babu Shrestha, Shalik Ram Subedi, Shankar Panthi and Huang Huasheng for their guideline and support. Finally, we acknowledge Department of National Parks and Wildlife Reserve Government of Nepal and the Annapurna Conservation Area Project (ACAP, Nepal) for providing permission to carry out the field work.

References

Ameztegui, A., Coll, L., Brotons, L., Ninot, J.M., 2016. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. Glob. Ecol. Biogeogr., http://dx.doi.org/10.1111/geb.12407, n/a–n/a.

Aryal, A., Hipkins, J., Ji, W., Raubeinhimer, D., Brunton, D., 2012. Distribution and diet of brown bear in Annapurna Conservation Area, Nepal. Ursus 23, 231–236.

Batllori, E., Gutiérrez, E., 2008. Regional tree line dynamics in response to global change in the Pyrenees. J. Ecol. 96, 1275–1288.

Bekker, M.F., 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. Arct. Antarct. Alp. Res. 37 (1), 97–107, http://dx.doi.org/10.1657/1523-0430(2005) 037[0097:PFBTEA]2.0.CO;2.

Beug, H.J., Miehe, G., 1999. Vegetation History and Human Impact in the Eastern Central Himalaya (Langtang and Helambu, Nepal) Diss. Bot. 318, Berlin, Stuttgart.

Bhattarai, S., Chaudhary, R.P., Quave, S.L., Taylor, R.S.L., 2010. The use of medicinal plants in the Trans-Himalayan arid zone of Mustang district, Nepal. J. Ethnobiol. Ethnomed. 6, 14, 10.1186/1746-4269-6-14.

Borgaonkar, H.P., Sikder, A.B., Ram, S., 2011. High altitude forest sensitivity to the recent warming: a tree-ring analysis of conifers from Western Himalaya India. Quatern. Int. 236, 158–166.

Bräuning, A., 2004. Tree-ring studies in the Dolpo-Himalaya (western Nepal). Tree Rings Archaeol. Climatol. Ecol. 2, 8–12.

Camarero, J.J., Gutiérrez, E., 2004. Pace and pattern of recent tree line dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Clim. Change 63, 181–200.

Camarero, J.J., Gutiérrez, E., 2007. Response of *Pinus uncinata* recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian System (NE Spain). Arct. Antarct. Alp. Res. 39, 210–217.

Chhetri, P.K., Cairns, D.M., 2015. Contemporary and historic population structure of Abies spectabilis at treeline in Barun valley, eastern Nepal Himalaya. J. Mt. Sci. 12 (3), http://dx.doi.org/10.1007/s11627-015-3454-5.

Cook, E.R., 1985. A time-series analysis approach to tree-ring standardization. In: Ph.D Dissertation. The University of Arizona Press, Tucson.

Cook, E.R., Kairiukstis, A., 1990. Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer Academic Press, Dordrecht.

Cook, E.R., Krusic, P.J., Jones, P.D., 2003. Dendroclimatic signals in long tree-ring chronologies from the Himalayas of Nepal. Int. J. Climatol. 23, 707e732.

Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7, 361–370.

Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J. Ecol. 95, 352–363.

Daniels, L.D., Veblen, T.T., 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85, 1284–1296.

Dubey, B., Yadav, R.R., Singh, J., Chaturvedi, R., 2003. Upward shift of Himalayan pine in western Himalaya, India. Current Sci. 85, 1135–1136.

Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea *(Dacrycarpus dacrydioides)*. N. Z. Nat. Sci. 16, 31–37.

Elliott, G.P., Kipfmueller, K.F., 2011. Multiscale influences of climate on upper treeline dynamics in the southern rocky mountains: USA: evidence of intraregional variability and bioclimatic thresholds in response to twentieth-century warming. Ann. Assoc. Am. Geogr. 101, 1181–1203.

Fritts, H.C., 1976. (Reprint, 2001) Tree Rings and Climate Caldwell, The Blackburn Press New Jersey.

Gaire, N.P., Dhakal, Y.R., Lekhak, H.C., Bhuju, D.R., Shah, S.K., 2011. Dynamics of *Abies spectabilis* in relation to climate change at the treeline ecotone in Langtang National Park. Nepal J. Plant Sci. 12, 220–229.

Gaire, N.P., Koirala, M., Bhuju, D.R., Borgaonkar, H.P., 2014. Treeline dynamics with climate change at the central Nepal Himalaya. Clim. Past 10, 1277–1290, http://dx.doi.org/10.5194/cp-10-1277-2014.

Gamache, I., Payette, S., 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. J. Biogeogr. 32, 849–862.

Ghimire, B.K., Lekhak, H.D., 2007. Regeneration of *Abies spectabilis* (D. Don) Mirb. in subalpine forest of upper Manang, north-central Nepal, in: Local Effects of Global Changes in the Himalayas: Manang, Nepal, edited by: Chaudhary RP, Aase TH, Vetaas O., Subedi, B.P., Tribhuvan Univ., Nepal, Univ. of Bergen, Bergen, Norway, 139–149.

Government of Nepal, 2010. Mustang District profile. District Statistical Office, Government of Nepal, Mustang District, Nepal, 87 p.

Grace, J., Berninger, F., Nagy, L., 2002. Impacts of climate change on the tree line. Ann. Bot. Lond. 90, 537–544.

Greenwood, S., Chen, J.C., Chen, C.T., Jump, A.S., 2014. Strong topographic sheltering effects lead to spatially complex treeline expansion and increased forest density in a subtropical mountain region. Glob. Change Biol. 20, 3756–3766.

Hagedorn, F., Shiyatov, S.G., Mazepa, V.S., Devi, N.M., Grigor'ev, A.A., Bartysh, A.A., Fomin, V.V., Kapralov, D.S., Terent'ev, M., Bugman, H., Rigling, A., Moiseev, P.A., 2014. Treeline advances along the Urals mountain range—driven by improved winter conditions? Glob. Change Biol., 3530–3543, http://dx.doi.org/10.1111/gcb.12613.

Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? a global meta-analysis of treeline response to climate warming. Ecol. Lett. 12, 1040–1049, http://dx.doi.org/10.1111/j.1461-0248.2009.01355.x.

Hofgaard, A., 1997. Inter-relationships between treeline position, species diversity land use and climate change in the central Scandes Mountains of Norway. Glob. Ecol. Biogeogr. Lett. 6, 419–429, http://dx.doi.org/10.2307/2997351.

Holtmeier, F.K., 2003. Mountain Timberlines: Ecology, Patchiness and Dynamics. Kluwer Academic Publishers, Dordrecht Germany.

Holtmeier, F.K., Broll, G., 2007. Treeline advance—driving processes and adverse factors. Landsc. Online 1, 1–33, http://dx.doi.org/10.3097/LO.200701.

Holtmeier, F.K., 2009. Mountain Timberlines: Ecology, Patchiness and Dynamics. Springer, Havixbeck, Germany, http://dx.doi.org/10.1007/978-3-319-02886-6_7.

IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen. S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., (Eds.), Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on climate change. Cambridge University Press, Cambridge, pp. 3–32.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. Ecoscience 14, 507–518.

Körner, C., 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer, Berlin, Germany.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732, http://dx.doi.org/10.1111/j.1365-2699.2003.01043.x.

Körner, C., 2012. Alpine Treelines. Functional Ecology of the High Elevation Tree Limits. Springer, Basel.

Kullman, L., 2001. 20th century climate warming and tree-limit rise in the Southern Scandes of Sweden. Ambio 30, 72–80.

Kullman, L., 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. J. Ecol. 90, 68–77, http://dx.doi.org/10.1046/j.0022-0477.2001.00630.x.

Kullman, L., 2007. Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973-2005: implications for tree line theory and climate change ecology. J. Ecol. 95, 41–52, http://dx.doi.org/10.1111/j.1365-2745.2006.01190.x.

Liang, E., 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, http://dx.doi.org/10.1890/13-1904.1, 140307191613003.

Liang, E., Wang, Y., Eckstein, D., Luo, T., 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. New Phytol. 190, 760–769, http://dx.doi.org/10.1111/j.1469-8137.2010.03623.x.

Lloyd, A.H., 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. Can. J. For. Res. 27, 936–942, http://dx.doi.org/10.1139/x97-028.

Lloyd, A.H., Fastie, C.L., 2002. Spatial and temporal variability in the growth and climate response of treeline trees in alaska. Clim. Change 52, 481–509, http://dx.doi.org/10.1023/A:1014278819094.

Lv, L.X., Zhang, Q.B., 2012. Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region. J. Plant Ecol. 5, 147–156, http://dx.doi.org/10.1093/jpe/rtr016.

Osborn, T.J., Briffa, K.R., Jones, P.D., 1997. Adjusting variance for sample-size in tree ring chronologies and other regional mean time series. Dendrochronologia 15, 89–99.

Qi, Z., Liu, H., Wu, X., Hao, Q., 2015. Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains northwestern China. Glob. Chang. Biol. 21, 816–826, http://dx.doi.org/10.1111/gcb.12703.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rinn, F., 2003. TSAP-Win: Time Series Analysis and Presentation for Dendrochronology and Related Applications. Version 0.55 User reference. Heidelberg, Germany (http://www.rimatech.com).

Sano, M., Furuta, F., Kobayashi, O., Sweda, T., 2005. Temperature variations since the mid-18th century for western Nepal, as reconstructed from tree-ring width and density of *Abies spectabilis*. Dendrochronologia 23, 83e92.

Schickhoff, U., 2005. The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. In: Broll, G., Keplin, B. (Eds.), Mountain Ecosystems: Studies in Treeline Ecology. Springer, Berlin, Germany.

Schickhoff, U., 2011. Dynamics of mountain ecosystems. In: Millington, A., Blumler, M., Schickhoff, U. (Eds.), Handbook of Biogeography. Sage Publ., London, pp. 313–337.

Schickhoff, U., Bobrowski, M., Böhner, J., Bürzle, B., Chaudhary, R.P., Gerlitz, L., Heyken, H., Lange, J., Müller, M., Scholten, T., Schwab, N., Wedegärtner, R., 2015. Do Himalayan treelines respond to recent climate change? an evaluation of sensitivity indicators. Earth Syst. Dynam. 6, 245–265 www.earth-syst-dynam.net/6/245/2015/10.5194/esd-6-245-2015.

Schloss, C.A., Nunez, T.A., Lawler, J.J., 2012. Proc. Natl. Acad. Sci. U. S. A. 109, 8606–8611.

Sharma, E., Tsering, K., 2009. Climate change in the Himalayas: the vulnerability of biodiversity. Sustain Mt. Dev. 55, 10–12.

Shrestha, B.B., Ghimire, B., Lekhak, H.D., Jha, P.K., 2007. Regeneration of treeline Birch (*Betula utilis* D. Don) Forest in a Trans-Himalayan dry valley in central Nepal. Mt. Res. Dev. 27, 259–267, http://dx.doi.org/10.1659/mrdd.0784.

Shrestha, K.B., Hofgaard, A., Vandvik, V., 2014. Recent treeline dynamics are similar between dry and mesic areas of Nepal, central Himalaya. J. Plant Ecol., http://dx.doi.org/10.1093/jpe/rtu035.

Shrestha, M.R., Rokaya, M.B., Ghimire, S.K., 2005. Vegetation pattern of Trans-Himalayan zone in the North–West Nepal. Nepal J. Plant Sci. 1, 129–135.

Shrestha, U.B., Gautam, S., Bawa, K.S., 2012. Widespread climate change in the Himalayas and associated changes in local ecosystems. PloS One 7, e36741.

Stainton, J.D.A., 1972. Forests of Nepal. Hafner Publishing Company, New York.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-Ring Dating. The University of Chicago Press, Chicago, pp. 63.

Summers, D.M., Bryan, B.A., Crossman, N.D., Meyer, W.S., 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. Glob. Change Biol. 18, 2335–2348, http://dx.doi.org/10.1111/j.1365-2486.2012.02700.x.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H., Silkin, P.P., 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400 (6740), 149–151, http://dx.doi.org/10.1038/22087.

Vetaas, O.R., 2000. The effects of environmental factors on regeneration of *Quercus semecarpifolia* Sm. in central Himalay, Nepal. Plant Ecol. 146, 137–144.

Vittoz, P., Rulence, B., Largey, T., Freléchoux, F., 2008. Effects of climate and land-use change on the establishment and growth of Cembran Pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the central Swiss Alps. Arct. Antarct. Alp. Res. 40, 225–232.

Wang, T., Zhang, Q. Bin, Ma, K., 2006. Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. Glob. Ecol. Biogeogr. 15, 406–415, http://dx.doi.org/10.1111/j.1466-822X.2006.00233.x.

Wang, S.Y., Yoon, J.H., Gillies, R.R., Cho, C., 2013. What caused the winter drought in western Nepal during recent years? J. Clim. 26, 8241–8256, http://dx.doi.org/10.1175/JCLI-D-12-00800.1.

Wang, Y., Liang, E., Ellison, A.M., Lu, X., Camarero, J.J., 2015. Facilitation stabilizes moisture-controlled alpine juniper shrublines in the central Tibetan Plateau. Glob. Planet Change 132, 20–30, http://dx.doi.org/10.1016/j.gloplacha.2015.06.007.

Wigley, T., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201–213.

Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.S.J., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Glob. Change Biol. 10, 1724–1736.

Xu, J., Grumbine, R., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., Wilkes, A., 2009. The melting Himalayas: cascading effects of climate change on water biodiversity, and livelihoods. Conserv. Biol. 23, 520–530.

Yadav, R.R., Singh, J., Dubey, B., Chaturvedi, R., 2004. Varying strength of relationship between temperature and growth of high-level fir at marginal ecosystems in western Himalaya, India. Current Sci. 8, 1152–1156.