

# Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature?

ERYUAN LIANG,<sup>1,6</sup> BINOD DAWADI,<sup>1,2,3</sup> NEIL PEDERSON,<sup>4</sup> AND DIETER ECKSTEIN<sup>5</sup>

<sup>1</sup>Key Laboratory of Tibetan Environment Changes and Land Surface Processes and Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101 China

<sup>2</sup>Central Department of Hydrology and Meteorology, Tribhuvan University, Kathmandu, Nepal

<sup>3</sup>University of Chinese Academy of Sciences, Beijing 100049 China

<sup>4</sup>Tree Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, Palisades, New York 10964 USA

<sup>5</sup>Centre of Wood Sciences, University of Hamburg, Leuschnerstrasse 91, Hamburg 21031 Germany

**Abstract.** Birch (*Betula*) trees and forests are found across much of the temperate and boreal zones of the Northern Hemisphere. Yet, despite being an ecologically significant genus, it is not well studied compared to other genera like *Pinus*, *Picea*, *Larix*, *Juniperus*, *Quercus*, or *Fagus*. In the Himalayas, Himalayan birch (*Betula utilis*) is a widespread broadleaf timberline species that survives in mountain rain shadows via access to water from snowmelt. Because precipitation in the Nepalese Himalayas decreases with increasing elevation, we hypothesized that the growth of birch at the upper timberlines between 3900 and 4150 m above sea level is primarily limited by moisture availability rather than by low temperature. To examine this assumption, a total of 292 increment cores from 211 birch trees at nine timberline sites were taken for dendroecological analysis. The synchronous occurrence of narrow rings and the high interseries correlations within and among sites evidenced a reliable cross-dating and a common climatic signal in the tree-ring width variations. From March to May, all nine tree-ring-width site chronologies showed a strong positive response to total precipitation and a less-strong negative response to temperature. During the instrumental meteorological record (from 1960 to the present), years with a high percentage of locally missing rings coincided with dry and warm pre-monsoon seasons. Moreover, periods of below-average growth are in phase with well-known drought events all over monsoon Asia, showing additional evidence that Himalayan birch growth at the upper timberlines is persistently limited by moisture availability. Our study describes the rare case of a drought-induced alpine timberline that is comprised of a broadleaf tree species.

**Key words:** alpine timberline; *Betula utilis*; central Himalayas; climate sensitivity; dendroecology; drought; missing ring; Nepal; precipitation; pre-monsoon season; tree-ring width; warming.

## INTRODUCTION

Near the distribution boundaries of tree species, climate strongly controls tree physiological and population dynamic processes (Malanson 2001, Körner 2003, Holtmeier and Broll 2005, Nagy and Grabherr 2009). Based upon notable similarities in various temperature parameters at treelines worldwide (Jobbágy and Jackson 2000, Grace et al. 2002, Körner and Paulsen 2004), it was proposed that the growing season temperature limits tree growth both at arctic and at alpine treelines/timberlines (e.g., Körner and Paulsen 2004, Wieser and Tausz 2007, Voelker 2011). This has been supported by dendroclimatic studies (e.g., Jacoby and D'Arrigo 1989, Payette et al. 1989, Villalba et al. 1997, Camarero et al. 2000, Mäkinen et al. 2000, Frank and Esper 2005, Luckman and Wilson 2005, Liang et al. 2009, Salzer et

al. 2009, Ettinger et al. 2011) as well as by seasonal cambial activity studies (e.g., Rossi et al. 2008, Seo et al. 2013). However, tree growth at timberlines not only depends on the growing season temperature, but also occasionally on winter temperatures that can cause frost drought in evergreen conifers (Oberhuber 2004, Mayr et al. 2006, Elliott 2012). In exceptional cases, timberline trees can even suffer from drought stress during the growing season (Tranquillini 1979, Leuschner 1996, Yang et al. 2013). Drought-induced alpine timberlines can be found not only on tropical and warm-temperate oceanic islands like on Mt. Teide, Tenerife (Leuschner 1996, Gieger and Leuschner 2004), but also at high-elevation subtropical treelines in Mexico (Biondi 2001), northwestern Argentina (Morales et al. 2004), and the central Andes (Daniels and Veblen 2004, Lara et al. 2005). However, little is known about whether such cases can also be observed at alpine timberlines in mid-latitudes, such as in the Himalayas and on the Tibetan Plateau, where the highest natural timberlines in the Northern Hemisphere can be found (Fang et al. 1996, Miede et al. 2007, Liang et al. 2011).

Manuscript received 10 October 2013; revised 21 February 2014; accepted 4 March 2014. Corresponding Editor: F. C. Meinzer.

<sup>6</sup> E-mail: liangey@itpcas.ac.cn

Dendroclimatic studies in high-elevation forests across the Tibetan Plateau indicate that the growth of conifers is primarily limited by temperature in the previous winter and/or in the current summer (Bräuning 2001, Cook et al. 2003, Liang et al. 2008). In particular, the growth of juniper, fir, and spruce trees at alpine timberlines in semihumid and humid areas on the southeastern Tibetan Plateau tends to be inhibited by low summer temperature (Gou et al. 2008, Liang et al. 2009, Zhu et al. 2011). In contrast, at alpine timberlines in semiarid areas on the northeastern Tibetan Plateau, growth of juniper is primarily limited by low winter temperature (Liu et al. 2005, Zhu et al. 2008, Shao et al. 2010). However, soil moisture availability can also become a constraint on tree growth at the upper timberlines on arid sites on the northern Tibetan Plateau (Yang et al. 2013).

Up to now, coniferous tree species have mostly been studied at timberlines, whereas birch (*Betula*), as an ecologically important and widespread broadleaf alpine and latitudinal timberline genus, remained mainly out of focus. At the northern timberline in Sweden (Eckstein et al. 1991, Kullman and Öberg 2009) and at the alpine timberlines in northeast China (Yu et al. 2005) and central Japan (Takahashi et al. 2005), birch growth is reported to be primarily controlled by temperature. As Himalayan birch (*Betula utilis* D. Don) dominates a wide area of the Himalayas (Zobel and Singh 1997), it is necessary to investigate constraints on the growth of this species as well. Himalayan birch forms an abrupt treeline from 3900 to 4200 m above sea level (asl). Such treelines are rare globally and have not been well studied (Harsch and Bader 2011). Due to its poor accessibility and difficulties in tree-ring cross-dating, little is known about its growth performance (Bräuning 2004, Bhattacharyya et al. 2006, Dawadi et al. 2013).

The objectives of our study, therefore, were to initialize a tree-ring network for Himalayan birch at its upper timberline in the central Himalayas and to identify the climatic factor(s) determining its radial growth. Based on the fact that precipitation in the Himalayas decreases with increasing elevation above 2000–3000 m asl (Putkonen 2004, Ichiyangi et al. 2007), we posit that the growth of birch at timberline might be more strongly limited by poor moisture availability than by low temperature.

## METHODS

### *Study area and climate*

Our study sites were located in high-elevation nature reserves (Sagarmatha, Langtang, and Manaslu) along three valleys in central Nepal and near well-known mountain peaks, such as Mount Everest (8848 m), Langtang Lirung (7246 m), and Manaslu (8150 m; Fig. 1). These reserve areas can be reached with an off-road vehicle or a small airplane. However, accessing the highest birch forests takes another 4–6 days of climbing,

which likely contributes to the dearth of studies on this species.

The Himalayas are situated in a transition area between subtropical and temperate mountains (Ichiyangi et al. 2007). The Nepalese climate is influenced by both maritime and continental factors, with the eastern and central parts of the country being exposed to the flow of the southeast monsoon (Putkonen 2004). The Tropical Rainfall Measuring Mission (TRMM) satellite, since its launch in November 1997, shows altitude-dependent variations in precipitation in the Nepal Himalayas (Fig. 2; NASA GES DISC; data *available online*).<sup>7</sup> Consequently, TRMM estimates of annual precipitation indicate an increase from lowland areas up to around 2000 m, followed by a decrease northward with increasing elevation. In the mid-elevation belt, between 2000 and 3000 m, annual precipitation is slightly higher than 2000 mm, and at around 4000 m it ranges from 750 to 1000 mm. Precipitation also varies at smaller scales depending on the local wind circulation and on whether a site is located on a windward or leeward slope (Barr 2008).

Instrumental records in the Langtang and Khumbu valleys as well as in the Mt. Everest area confirm the general pattern of altitude-dependent precipitation (Barr 2008). Annual precipitation is around 3500 mm in the Langtang valley (from 1600 to 2600 m; Dhar and Nandargi 2000), and around 780 mm (recorded from 2005 to 2008) at Kyangjing (3920 m), which is close to our birch timberline site LT1. South of Mt. Everest, at 2600 m, the annual sum of precipitation ranges from 2300 to 2600 mm. Precipitation then decreases to 1000 mm or less from 3450 to 3850 m, whereas on the Khumbu Glacier (5300 m) it is only 450 mm (Dhar and Nandargi 2000). As recorded by the high-altitude Pyramid meteorological station (5050 m), 12 km southwest of Mt. Everest, the average annual precipitation was 465 mm from 1994 to 1999 (Bollasina et al. 2002) and 343 mm from 2005 to 2008; very little precipitation fell from December to April during these periods (Fig. 3).

Annual maximum, mean, and minimum temperatures at Kyangjing are around 9.4°C, 3.7°C, and −0.2°C, respectively; the temperature in the warmest month (July) is around 9.8°C, i.e., close to the 10°C isotherm, which is generally taken to estimate the treeline position (Tranquillini 1979). The mean temperature during the growing season from May to September is 8.2°C, which is within the range of the average gridded growing season temperatures at timberlines (Voelker 2011).

### *Study species*

Himalayan birch is endemic to the Himalayas and occurred at elevations up to 1800 m during the Pliocene (~5–2.5 million years before present), a period of

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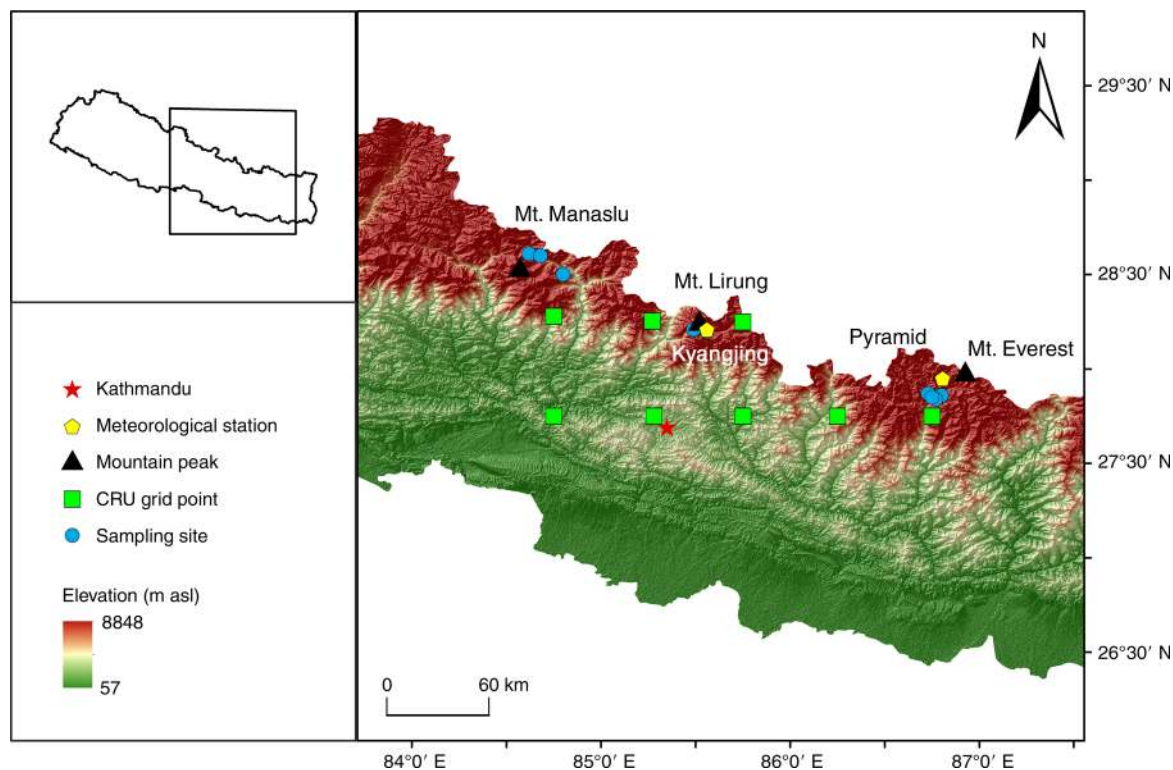


FIG. 1. Location of Himalayan birch sampling sites and climatic research unit (CRU) grid points, as well as high-elevation meteorological stations at Kyangjing in the Langtang valley and at Pyramid in the Mt. Everest area in the Nepal Himalayas. Elevation is given in meters above sea level (asl).

global-scale cooling and drying, but today it grows above 3000 m (Vishnu-Mittre 1984), and is generally found in rain-shadow locations. Between 3500 and 3900 m, Himalayan birch grows in forests mixed with *Abies spectabilis*. Pure Himalayan birch forests, with an understory of *Rhododendron campanulatum* up to 3 m tall, occur between 3900 and 4200 m, where they are quite undisturbed due to the difficult access. In the open terrain above treeline, *Rhododendron anthopogon* and *Cassiope fastigiata* up to 30 cm high are dominant.

We focused on undisturbed pure Himalayan birch forests in a forest belt from 3900 to 4150 m, which form an abrupt treeline without a krummholz zone (Fig. 4). The mean total coverage in this vegetation zone amounts to more than 30%. Despite some birch seedlings and saplings under the forest canopy, recruitment was generally low.

#### *Tree-ring sampling, cross-dating, and standardization*

Increment cores were taken at nine Himalayan birch timberline sites from 3900 to 4150 m in Sagarmatha (four sites), Langtang (two sites), and Manaslu (three sites), where natural Himalayan birch timberlines are highly representative of those in the central Himalayas (Table 1). Apart from one site (SKB3) at a southeast-facing slope in the Sagarmatha National Park, all other sites are located in the rain shadow on southwest- or

west-facing slopes. All sites are characterized by a thin layer of rocky soil. At each site, 15–30 dominant birch trees between 8 and 12 m in height and 50 and 80 cm in diameter were selected for coring, and one to two cores were taken from each tree. Some cores were excluded due to unclear tree-ring boundaries. Altogether, we included 292 cores from 211 living trees.

Tree-ring widths were measured to an accuracy of 0.01 mm using a LINTAB measuring system (Rinntech, Heidelberg, Germany); locally missing rings were given a value of zero. Ring boundaries in birch are faint and delineated by one cell row of terminal axial parenchyma (Fig. 5), which is often filled with brownish extractives. Boundaries were more easily distinguished when the core surface was kept moist. The quality of cross-dating and measurements was checked using the program COFECHA (Holmes 1983).

The tree-ring width series of each individual tree was transformed to a dimensionless time series by the program ARSTAN (Cook 1985) using a smoothing spline of 67% of the series length. The “two-thirds spline” approach to standardization removes growth trends related to the geometry of adding radial increments on an increasing stem diameter and to stand dynamics (Cook and Peters 1981). The resulting time series of each site were averaged into site standard chronologies.

### Analyses

Several descriptive statistics, including mean series intercorrelation ( $R_{\text{BAR}}$ ) and expressed population signal (EPS; Briffa and Jones 1990) were used to qualify the site chronologies within a common interval from 1840 to 2009.  $R_{\text{BAR}}$  is the mean correlation coefficient among the tree-ring series of a site, while EPS assesses the degree to which a site chronology represents a hypothetical chronology based on an infinite number of cores; an  $\text{EPS} \geq 0.85$  is often taken to identify the reliable part of a tree-ring chronology (Briffa and Jones 1990). Principal component analysis (PCA) was conducted using all nine site chronologies to identify the extent of common growth variation through time. PCA decomposes the total variance of all tree-ring widths into its principal components; the first principal component (PC1) accounts for as much of the variability in the data as possible.

To determine the climate–tree-growth relationships, correlations with bootstrapped confidence intervals (Biondi and Waikul 2004) were calculated between the nine site chronologies and their PC1 (as predictands), and monthly climate data (as predictors) obtained from the CRU TS 3.0 (climatic research unit, time-series data sets, version 3.0; Mitchell and Jones 2005) at  $0.5^\circ$  spatial resolution from 1950 to 2009. An average of climate data sets from eight CRU grids was used to represent the regional monthly mean temperature and monthly sums of precipitation. These values showed high correlations with the instrumental records at Pyramid (5050 m) from 1994 to 2008 (for temperature,  $r = 0.92$ ,  $n = 180$  months,  $P < 0.0001$ ; for precipitation,  $r = 0.82$ ,  $n = 180$  months,  $P < 0.0001$ ). Thus, the regionally averaged gridded temperature and precipitation data reflected the climatic conditions in our study area well. The climate/growth correlation analysis was performed for a 15-month period from the previous July to the current September.

Partial correlation was used to measure the linear relationship between two variables, such as tree-ring widths and pre-monsoon precipitation, after having excluded the effect of a third variable, such as pre-monsoon temperature.

### RESULTS

#### *Cross-dating, occurrence of locally missing rings, and chronology statistics*

Of the 211 Himalayan birch trees, three were more than 400 years old, while 19 were more than 300 years old. Mean tree-ring width was  $0.81 \pm 0.53$  mm (mean  $\pm$  SD). Narrow rings occurred in 1710, 1813, 1954, 1967, 1968, 1974, 1975, 1995, 1999, 2000, 2003, and 2004 (Fig. 6), thus showing a distinct accumulation in the 20th and in the beginning of the 21st century. However, there were also earlier periods characterized by sustained low growth, e.g., from 1756 to 1767, 1789 to 1795, and 1809 to 1821, as reflected in the regional chronology (RC; Fig. 6).

From a total of 56 157 tree rings identified by cross-dating across all sites, 414 (0.74%) were locally missing. During the past 300 years, locally missing rings were most frequent in the most recent six decades, with the strongest examples in 1954 (6.0%), 1968 (7.9%), 1974 (6.1%), 1975 (4.1%), 1995 (7.6%), 1999 (14.7%), 2000 (12.1%), 2003 (17.1%), and 2004 (18.1%; Fig. 7). This phenomenon does not appear to be age-dependent. For example, the locally missing rings in 2004 were fairly evenly distributed over all age classes, from 70 to 370 years, and no significant ( $P > 0.05$ ) age-dependent trend was found. In particular, the three trees older than 400 years did not have a locally missing ring in 2004 (Fig. 7). Locally missing rings occurred more often at leeward sites than at windward sites. In the Langtang valley, the southwest-facing slope (site LT4) receives more solar radiation and might experience stronger evaporation than the west-facing slope (site LT1). As a result, more rings were locally missing at LT4 (2.02% missing rings) than at LT1 (0.51%). The percentages of locally missing rings in the Sagarmatha National Park sites were 0.5% at SKB1 and SKB2 in the rain shadow on a southwest-facing slope, 0.24% at SKB3 on a windward southeast-facing slope, and 0.14% at SKB4 on a northwest-facing slope with potentially less evaporation.

The occurrence of locally missing rings was significantly correlated with warm and dry conditions during the pre-monsoon season (Fig. 8). In particular, the frequency time series of locally missing rings showed a significant and negative correlation with pre-monsoon precipitation ( $r = -0.31$ ,  $P < 0.05$ ,  $n = 60$ ) and a significant and positive correlation with pre-monsoon temperature ( $r = 0.30$ ,  $P < 0.05$ ,  $n = 30$ ). Partial correlation coefficients for the same relationships were still significant ( $r = 0.26/0.28$ ,  $P < 0.05$ ) when the effects of temperature or precipitation, respectively, were excluded.

$R_{\text{BAR}}$  within each of the nine tree-ring site chronologies ranged from 0.28 to 0.35. Interseries correlation within the sites ranged from 0.48 to 0.56, and was 0.42 between all 292 tree-ring series. EPS values of  $\geq 0.85$  occurred between 1710 and 1840 m across all sites (Table 1, Fig. 6). The first principal component (PC1) of all nine chronologies represented 49.0% of the variation in the 1840–2009 common period. All chronologies load positively on PC1.

#### *Climate–tree-growth relationships*

Variation in growth of timberline Himalayan birch was most strongly correlated with pre-monsoon moisture availability, as shown by consistently positive correlations with precipitation from March to May; significant correlations ( $P < 0.05$ ) were calculated for at least one of these three months at the nine sites (Fig. 9). Summing precipitation from March to May resulted in significant correlations with all chronologies, although correlations were stronger on southwest-facing slopes ( $P$



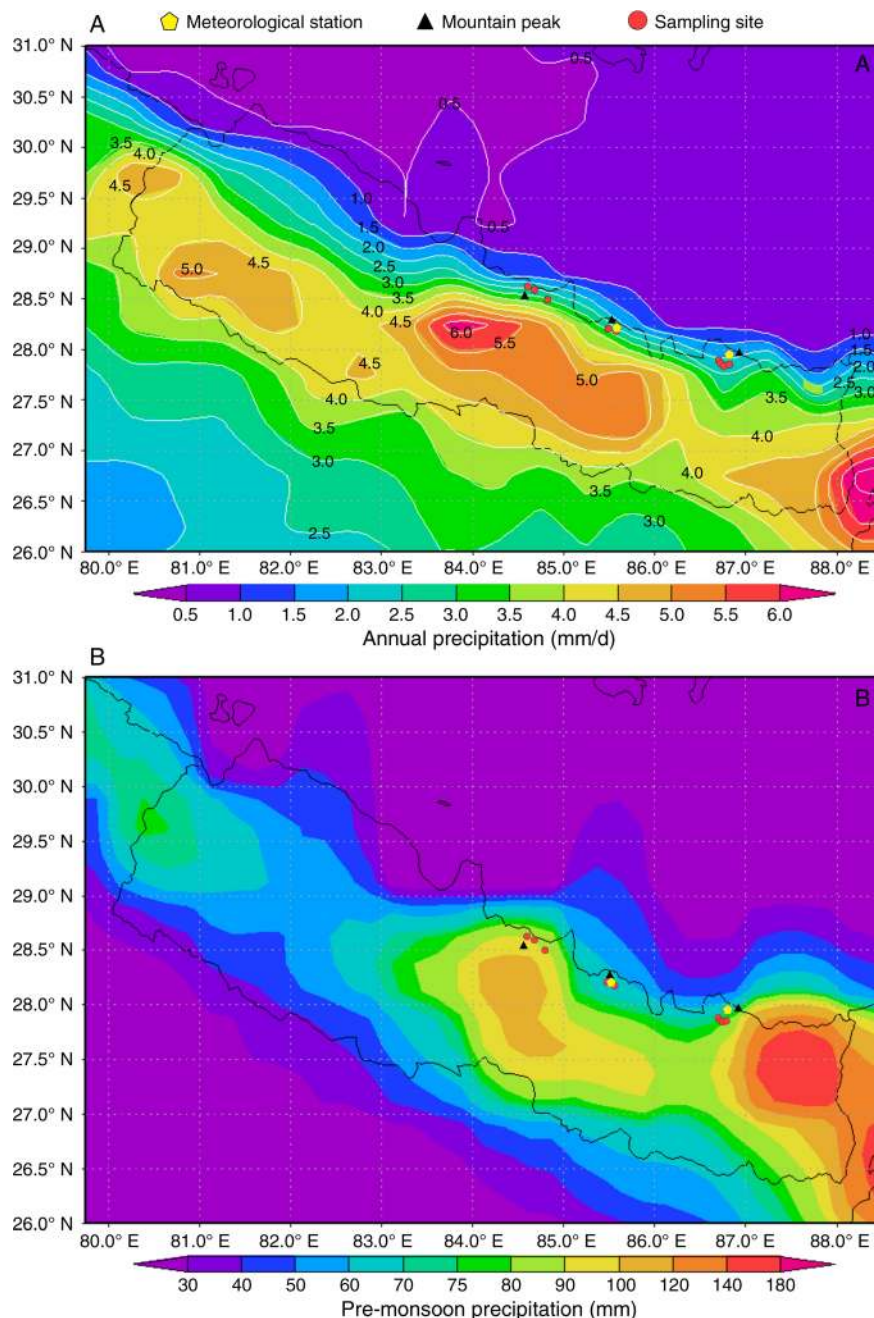


FIG. 2. Spatial distribution of (A) annual precipitation (mm/d) and (B) pre-monsoon precipitation (mm) in the study area, based on Tropical Rainfall Measuring Mission composite climatology data.

$< 0.001$ ) compared to a site on windward southeast-facing slope (SKB3;  $P < 0.05$ ) and an additional site on a northeast-facing slope (MPB1;  $P < 0.05$ ). All chronologies showed negative correlations with temperature from March to May, with significant coefficients for May at LT4, April at SKB2 and MPB1, and March and April at SKB3. The partial correlation still showed a significant correlation ( $P < 0.05$ ) between the SKB2 and LT4 site chronologies and temperature by excluding the

effect of precipitation during the pre-monsoon season. Unexpectedly, the correlation between temperature and precipitation during the pre-monsoon season was insignificant ( $r = -0.20$ ,  $P > 0.05$ ).

PC1 was strongly and positively correlated with pre-monsoon precipitation from 1950 to 2009 ( $r = 0.55$ ,  $P < 0.0001$ ; Fig. 8). In contrast, PC1 was negatively correlated with the mean temperature from March to May ( $r = -0.31$ ,  $P < 0.05$ ).

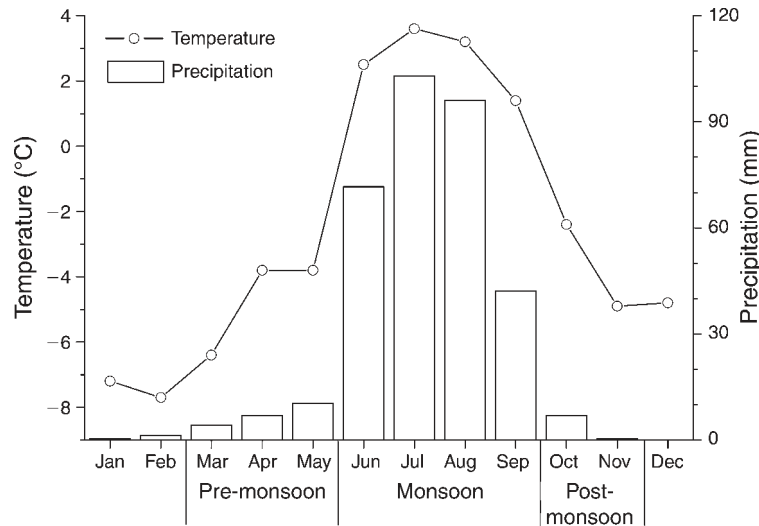


FIG. 3. Monthly mean temperature and sum of precipitation at the Pyramid station ( $27^{\circ}57' \text{ N}$ ,  $86^{\circ}12.6' \text{ E}$ , 5050 m asl), based on the average from 2005 to 2008; annual mean temperature,  $-2.5^{\circ}\text{C}$ , average sum of annual precipitation, 343 mm.

## DISCUSSION

### *Growth response of Himalayan birch to climate at timberline*

Abrupt treelines, as in our case the Himalayan birch treeline, are often thought to be rather unresponsive to climate (Cuevas 2000, Danby and Hik 2007, Harsch and Bader 2011). But we found just the contrary to be true; Himalayan birch growth responded directly to the availability of moisture during the pre-monsoon season. These findings give further support that early-year moisture matters to this species. Shrestha et al. (2007) reported that the regeneration of Himalayan birch depends on the amount of snow melting in spring. This growth response clearly differs from the behavior of high-elevation conifers close to or in the belt of maximum precipitation at  $\sim 3000 \text{ m}$  in the central Himalayas (Cook et al. 2003). The response of Himalayan birch to climate also differs from the response of most alpine and arctic timberline trees, where growth is primarily limited by low temperature (Bräuning 2001, Oberhuber 2004, Zhu et al. 2011). In our study, Himalayan birch responded similarly to trees at timberlines in the subtropics (Leuschner 1996, Biondi 2001, Morales et al. 2004) and in the central Andes of Chile (Daniels and Veblen 2004, Lara et al. 2005), where less precipitation means stronger solar radiation and evaporation. The similarity in our findings to those at subtropical and tropical treelines is reasonable, given that our Himalayan birch sites are nearing the average value ( $\sim 4150 \text{ m}$ ) of subtropical/tropical treelines (Voelker 2011). Himalayan birch also shares this similarity with an alpine juniper shrub whose growth is strongly limited by moisture in the early growing season at an extremely high elevation of up to 4800 m in central

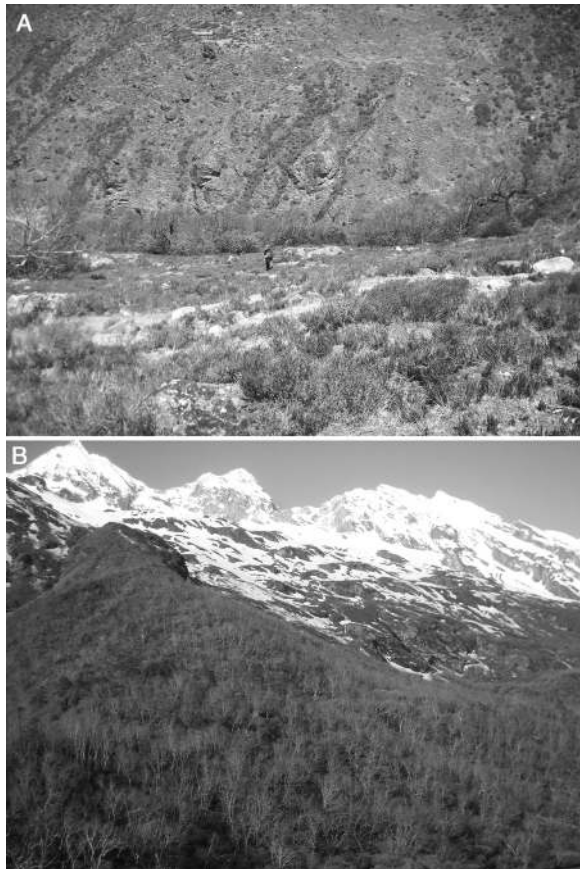


FIG. 4. Birch forests forming abrupt treelines in the (A) Sagarmatha and (B) Manaslu conservation areas.

TABLE 1. Site information and some major statistics for Himalayan birch in the Sagarmatha National Park (sites SKB1–4), Langtang National Park (sites LT1, LT4), and Manaslu Conservation Area (sites MPB1, MSB1, MSB2) in the central Himalayas.

Site	Latitude (°N)	Longitude (°E)	Elevation (m asl)	Slope	$R_{\text{BAR}}$	EPS $\geq 0.85$ since year
SKB1	27.86	86.8	4150	8° NW	0.32	1710
SKB2	27.84	86.77	3950	10° W	0.35	1785
SKB3	27.87	86.73	4010	12° SE	0.33	1790
SKB4	27.85	86.75	3920	15° SW	0.32	1780
LT1	28.12	85.34	4050	10° W	0.28	1835
LT4	28.13	85.32	3900	8° SW	0.31	1815
MSB1	28.61	84.63	4020	10° NE	0.31	1805
MSB2	28.61	84.86	3980	8° SW	0.25	1840
MPB1	28.5	84.8	3950	10° SE	0.34	1740

Notes: Elevation is presented in meters above sea level (m asl). EPS stands for expressed population signal, and all years listed are AD. Slope is presented in degrees and aspect (NW, northwest; W, west; SE, southeast; SW, southwest; NE, northeast).  $R_{\text{BAR}}$  represents the mean series intercorrelation.

Tibet (Liang et al. 2012). The climate–tree-growth relationship obtained in this study is also similar to that in semiarid forests (Fritts 1974, Zhang et al. 2003, Sheppard et al. 2004, Shao et al. 2005, Cook et al. 2010, Voelker 2011, Yang et al. 2013), as well as in the forest-steppe ecotone in Inner Asia (Pederson et al. 2001, Dulamsuren et al. 2010, Liu et al. 2013), where precipitation in the early growing season is a major determinant of tree growth.

In spite of the high elevation, moisture availability in the pre-monsoon season overrides any effect expected from low temperature as a control of Himalayan birch growth at timberline. Dry environmental conditions above the treeline of Himalayan birch is evidenced by the occurrence of *Cassiope fastigiata* dwarf shrubs, a drought-tolerant species. A temperature inversion restricts the rise of humid air masses further upslope, and hence causes a dry climate at high elevations, similar as at some timberlines on tropical and warm-temperate oceanic islands (Leuschner 1996). As recorded by the Pyramid meteorological station close to Mt. Everest, pre-monsoon precipitation amounts to 24 mm, accounting for only 7.0% of the annual precipitation. An extremely dry pre-monsoon season followed by above-average precipitation from June to August, for example in 2003, still results in a narrow or even missing ring in Himalayan birch trees. Phenological observations of conifers exposed to drought also revealed that moisture availability in the early growing season determines the total annual aboveground biomass, although the physiological limitation of growth is complex (Swidrak et al. 2013). Additionally, a recent study that controlled soil moisture and temperature showed that water deficit prior to the growing season can cause a 2–4 week delay to completely restoring cambial activity of *Picea mariana* saplings, resulting in a narrow ring (Balducci et al. 2013). We also have to keep in mind that the annual resolution of the ring widths may preclude a deeper understanding on the effects of moisture availability on tree growth (Voelker et al. 2014). Monitoring of the intra-annual cambial activity and in

situ acquisition of micrometeorological data will be a further step toward a better understating of constraints of pre-monsoon weather conditions on Himalayan birch growth at timberline.

Interestingly, the climate–growth relationships of timberline Himalayan birch are more similar to the climate responses of many broadleaf species near or at

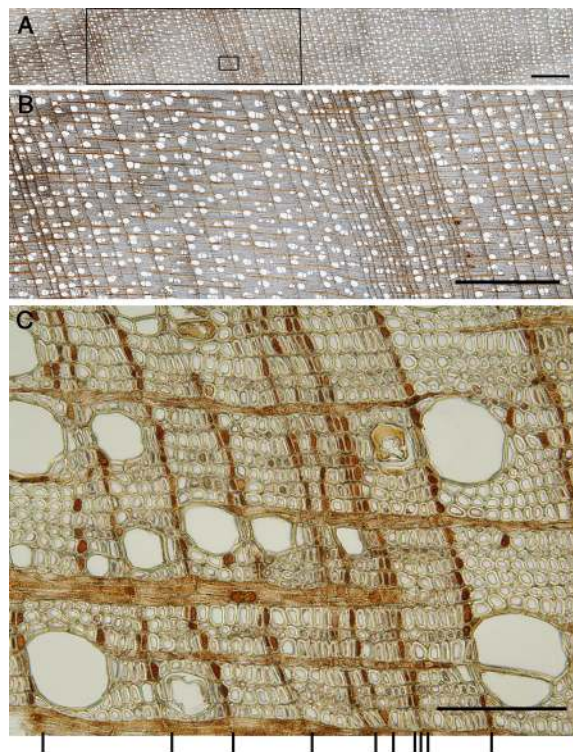


FIG. 5. Cross-section of Himalayan birch in original wood color; the two rectangular frames in A show the areas enlarged in B and C. The tree-ring borders are delineated by (C) one row of terminal axial parenchyma cells, often filled with brownish extractives; short vertical lines along the bottom edge mark the tree-ring widths. Scale bars in A and B are 2 mm, and in C are 0.2 mm.



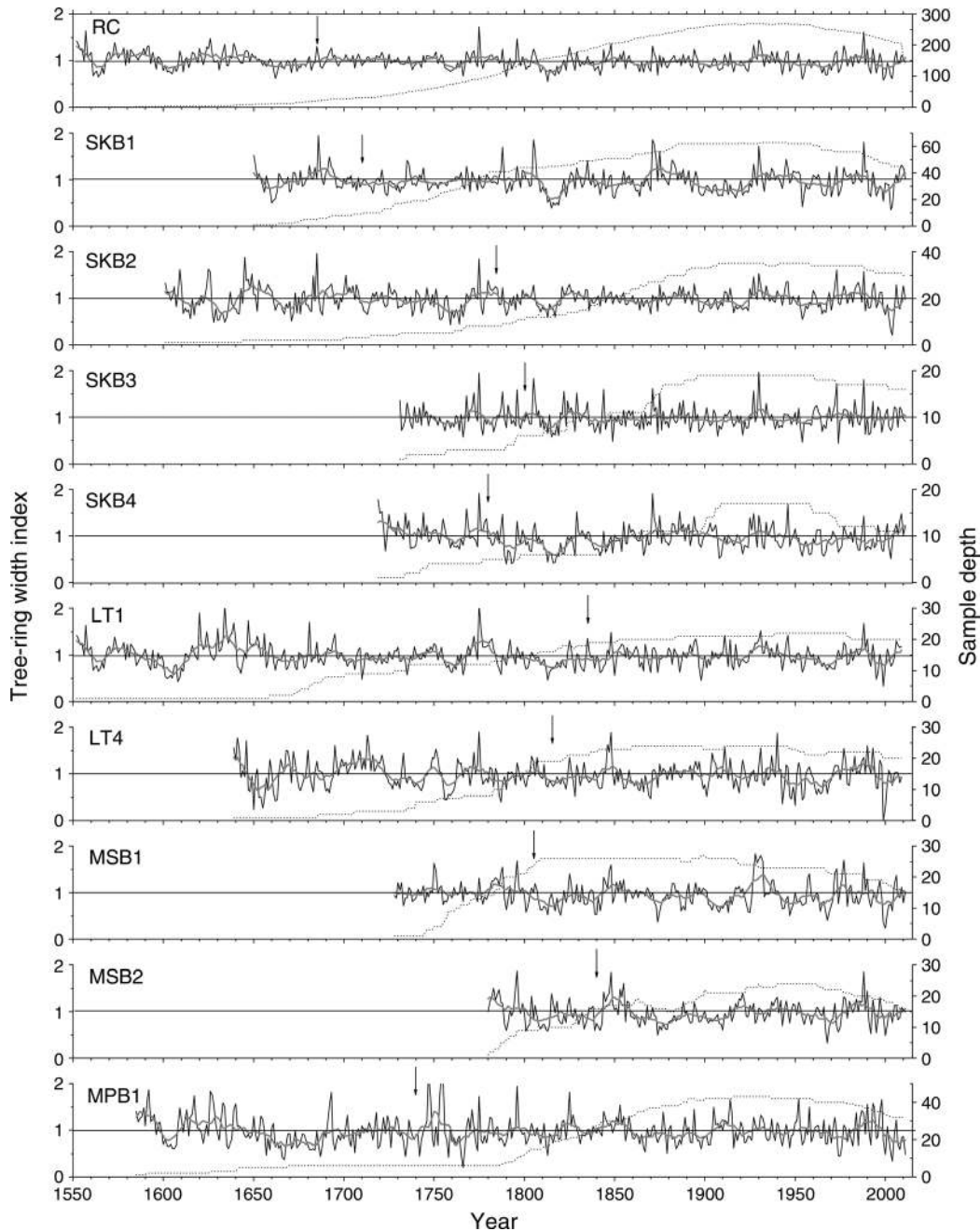


FIG. 6. Nine tree-ring site chronologies for Himalayan birch in the Langtang (study sites LT1, LT4), Sagarmatha (sites SKB1, SKB2, SKB3, and SKB4), and Manaslu conservation areas (sites MSB1, MSB2, and MPB1) and their regional average chronology (RC) in the central Himalayas; number of individual tree-ring series included (sample depth); vertical arrows indicate years when expressed population signal  $\geq 0.85$ .

“poleward” range margins than of coniferous species at timberlines; by “poleward,” we mean the northern range margins in the Northern Hemisphere and southern range margins in the Southern Hemisphere. The growth of some coniferous species at poleward margins is often sensitive to low temperature (e.g., Cook et al. 1998, Pederson et al. 2004, Huang et al. 2010). In contrast,

Tardif et al. (2001) in southwestern Quebec and LeBlanc and Terrell (2011) across eastern North America found that broadleaf trees were less limited by low temperatures than by moisture availability. Further, four broadleaf species near a poleward range margin appeared to be more limited by drought (Pederson et al. 2013). Our results from Himalayan birch trees add



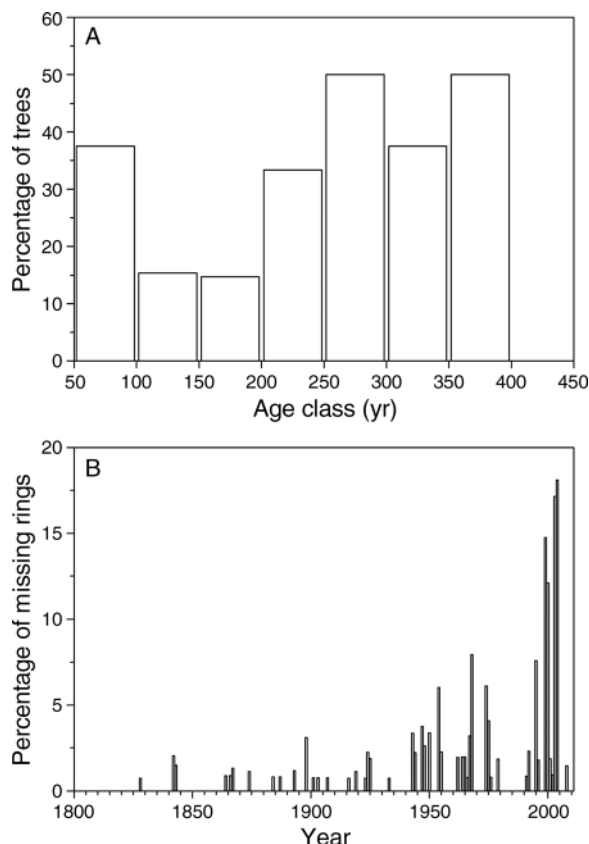


FIG. 7. Percentage of (A) trees with locally missing rings in 2004 in different age classes, and (B) frequency of locally missing rings since AD 1800 at the nine study sites.

additional evidence to support the hypothesis that broadleaf species at timberline or poleward range margins are typically more limited by moisture availability than by low temperatures.

#### *Missing rings as evidence for moisture stress*

The occurrence of missing rings in Himalayan birch indicates that drought stress sometimes controls its survival limit. In particular, dry and warm pre-monsoon seasons appear to cause missing rings, or periods of no cambial growth on parts of the stem. During the instrumental period, after 1960, seven years with a high percentage of missing rings coincide with pre-monsoon droughts in Nepal. An outstanding example of this is 1999, when crop failures were reported across the country (Sigdel and Ikeda 2010). The soil water availability at high altitudes is highly dependent on topography, soil substrate, and exposure (Barr 2008). More frequent missing rings at leeward sites (southwest exposure) than at windward sites (west exposure) provide strong evidence for a linkage between birch growth and the amount of local moisture availability. In addition, Himalayan birch trees of low vigor or poor competitive power might be more susceptible to the

stresses that cause missing rings. In contrast to our findings, however, no locally missing rings were found for temperature-sensitive conifers in the central Himalayas (Cook et al. 2003, Sano et al. 2005) and at timberlines of the southeastern Tibetan Plateau (e.g., Liang et al. 2009, Zhu et al. 2011). Thus, the occurrence of missing rings in Himalayan birch offers additional evidence that its growth is precipitation-controlled, as shown for semiarid forests on the Tibetan Plateau (e.g., Zhang et al. 2003, Sheppard et al. 2004, Shao et al. 2005, 2010).

There is much evidence that the previous 50 years on the Tibetan Plateau were the warmest during the last 1000 years (Yang et al. 2003, Liu et al. 2005, 2009, Zhu et al. 2008). As reported for other regions, the recent warming intensified growth decline and tree mortality (Allen et al. 2010, Peng et al. 2011, Liu et al. 2013). The increasing frequency of missing rings in recent decades might result from increased moisture stress associated with a general warming trend. Additionally, there has been a decrease in precipita-

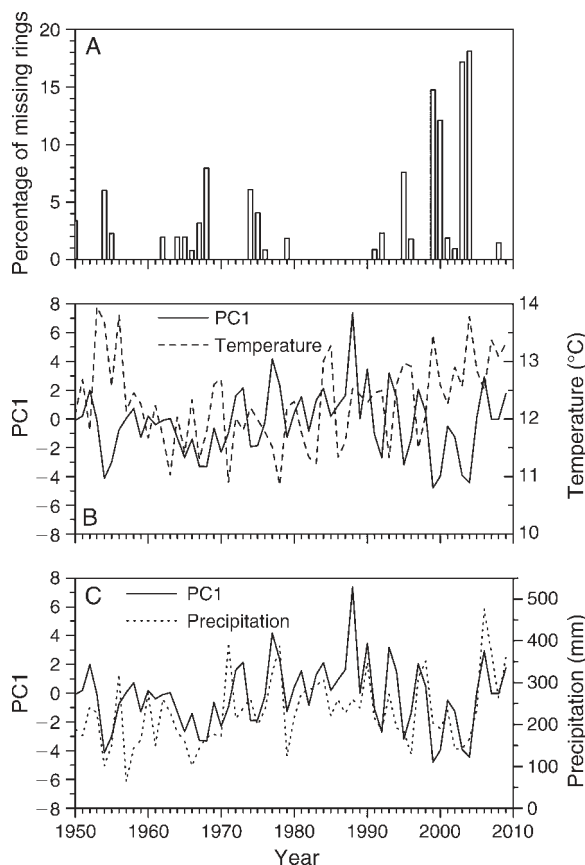


FIG. 8. Comparison of (A) the frequency of locally missing rings, (B) the first principal component (PC1) of nine Himalayan birch chronologies and pre-monsoon temperature, and (C) PC1 of nine Himalayan birch chronologies and pre-monsoon precipitation over the period 1950 to 2009.

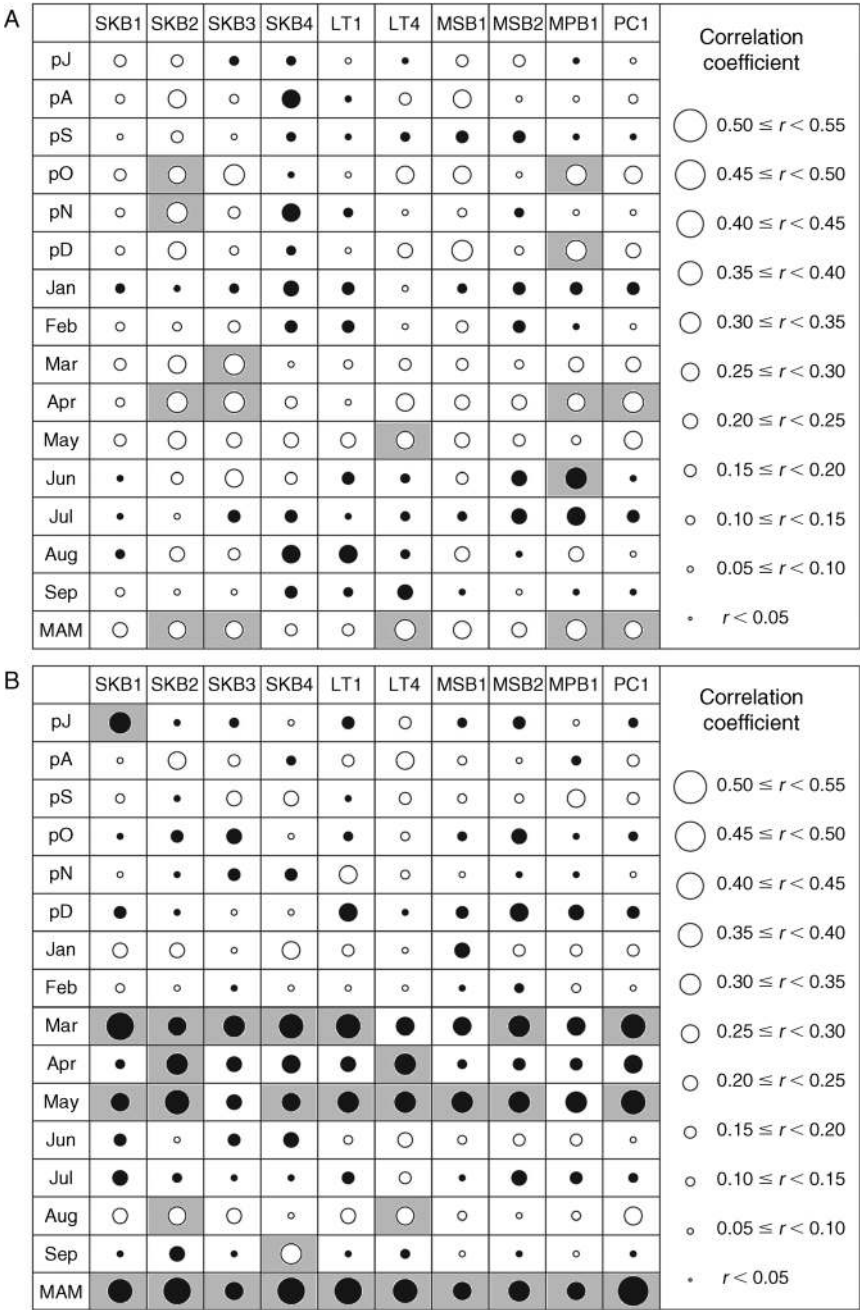


FIG. 9. Correlations between nine standard ring-width chronologies (see Fig. 6 for definitions), their PC1, and (A) monthly mean temperature and (B) monthly sum of precipitation from July of the previous year to September of the current year. Fields pJ–pD signify July–December of the previous year; MAM means the mean temperature and the sum of precipitation from March to May in panels (A) and (B), respectively. Solid circles indicate positive and open circles negative correlations. Background shading represents significance at the  $P < 0.05$  level. The circle size shows the strength of correlation whereby the smallest circle denotes  $r < 0.05$  and the largest circle denotes  $0.50 \leq r < 0.55$ , with an interval of 0.05.

tion and retreat of glaciers in the central Himalayas (Yao et al. 2012). As a consequence, future moisture stress may cause similar dieback events and possibly even downslope tree range contractions of Himalayan birch.

*Sustained moisture stress in a long-term view*

Sustained low growth intervals prior to the instrumental period coincide with historical megadroughts identified in monsoon Asia, including the Strange Parallels Drought (1756–1768), the East India Drought (1790–1796; e.g.,

Buckley et al. 2010, Cook et al. 2010, D'Arrigo et al. 2011), and the prolonged droughts during the 1810s and 1820s in the western Himalayas (Yadav 2011). This provides additional evidence that birch growth at the upper timberlines is persistently limited by moisture availability.

#### CONCLUSIONS

Growth of birch at its upper timberlines in the central Himalayas is limited by the amount of moisture during the pre-monsoon season. Additionally, narrow tree rings are associated with warm pre-monsoon seasons, presumably as a result of severe water deficits driven by higher vapor pressure deficits in the atmosphere. Such particular phenomena for the upper timberlines in the central Himalayas are largely due to the fact that precipitation decreases with increasing elevation above 2000–3000 m. It might be that Himalayan birch adapted as it evolved as a species. The increasing frequency of missing rings during the recent decades and their close coincidence with dry and warm pre-monsoon seasons, in particular on leeward sites, provides evidence that Himalayan birch at its upper distribution boundary is increasingly at risk for survival, and downslope range shifts could occur as a response to global-change-type droughts. The strong association between drought and growth of Himalayan birch at timberline also provides a rare opportunity to reconstruct variations in pre-monsoon precipitation over the past 400 years. This opportunity will allow for a better understanding of historic drought events in the central Himalayas.

#### ACKNOWLEDGMENTS

Funding for this research was provided by the National Basic Research Program of China (2010CB951301, 2012FY111400), the National Natural Science Foundation of China (41130529), and the Strategic Priority Research Program—Climate Change: Carbon Budget and Relevant Issues of the Chinese Academy of Sciences (XDA05090311) and the Third Pole Environment (TPE) program. We thank the Department of National Parks and Wildlife Conservation, the government of Nepal for granting permission to carry out this research, the Ev-K2-CNR Pyramid Meteorological Station (5050 m asl) for sharing climatic data, two reviewers for their valuable comments, and Sergej Kaschuro (Hamburg) for preparing the wood cross-sections.

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