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Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region

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Abstract

Aims

Forest growth and recruitment and their relationships to climate are complex. The aims of our study are (i) to examine the patterns in tree radial growth and recruitment along an altitudinal gradient in Mt. Everest region and (ii) to identify the climatic factors that are responsible to the observed patterns in tree growth and recruitment.

Methods

Four plots, each 30 × 60 m in size, were established from the lower to upper limits of the eastern Himalayan fir forest in Dingjie County of the Mt. Everest Nature Reserve, China. Dendrochronological techniques were applied to obtain information about the radial growth and age of the trees in the plots. Correlation analysis was used to identify the relationships between radial growth and recruitment of trees and climatic variables, i.e. monthly mean temperature and Palmer Drought Severity Index (PDSI). The population age structure was analyzed to investigate the recruitment history.

Important Findings

The timberline plot was characterized by significant tree recruitments in the recent three decades and sporadic recruitments in earlier periods. The other three plots showed recruitment pulses during 1880–1910 in Plot 3 700 m, during 1870–80 and 1920–30 in Plot 3 520 m and during 1900–40 in Plot 3 410 m. The recruitment of fir trees in the timberline was sensitive to summer (June–September) temperatures, but it was mainly controlled by episodic disturbances in lower altitudes. Fir radial growth in the upper two plots was positively correlated with previous winter and current August temperature. Fir radial growth at the two lower plots was positively correlated with PDSI from previous September to current September.

Keywords: tree rings • tree recruitment • age structure • disturbance • timberline dynamics

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INTRODUCTION

Tree growth and recruitment are two important ecological processes shaping the forest landscape. Variation in these processes is closely related to climate change and disturbances (Abrams *et al.* 1998; Gutiérrez *et al.* 2008; Nowacki and Abrams 1997). In subalpine areas, the impacts of climate and disturbance on forest growth and recruitment may become more complex due to changes in habitat conditions at different altitudes (Dalen and Hofgaard 2005; Germino *et al.* 2002; Stueve *et al.* 2009). There have been reports that tree recruitment is controlled mainly by climate in alpine treeline ecotones (Camareno and Gutiérrez 2004; Wang *et al.* 2006). Several consecutive years of high minimum summer temperatures and spring precipitation was found to be a main factor favoring the establishment of *Picea schrenkiana* following germination within the treeline ecotone in the central Tianshan Mountains, Northwestern China (Wang *et al.* 2006). Warmer summers encouraged regeneration of *Betula pubeseens* ssp. *tortuosa* at higher elevation in years between 1933 and 1939 in Scandinavia (Kullman 1993). Mild winters and moisture availability affected tree recruitment in Swedish Scandes and forest-grassland ecotones of Colorado (Kullman 2002). Disturbances such as fire, insect outbreak and grazing also played a role in shaping forest growth and recruitment in New Zealand and North America (Cullen *et al.* 2001; Lusk and Smith 1998; Veblen *et al.* 1994). It seems that the response of forest growth and recruitment to climate and disturbances is not a simple one but varies according to the types of forest and to the complexity of their climate conditions and disturbance regime (Abrams *et al.* 1998; Brown and Wu 2005; Cuevas 2002; Danby and Hik 2007; Gutiérrez *et al.* 2008; Veblen *et al.* 1994). This diversity in response pattern indicates a need to expand our observation both in space and in time.

Located on the southern Tibetan Plateau with five mountain peaks higher than 8 000 m above sea level, the Mount Everest Nature Reserve (27°48′–29°19′N, 84°27′–88°E) has a unique physiographic and forest landscape and is in a critical position to respond to global climate change. The Intergovernmental Panel on Climate Change (2007) report indicates that greater warming is expected to occur over the Plateau as compared to surrounding areas, with the largest warming at highest altitudes, e.g. over the Himalayas. East Himalayan fir (*Abies spectabilis* (D. Don) Spach) is a widely distributed tree species in subalpine ecotone of this region (Xu 2001). Because of the high elevation and protection in the Nature Reserve, the forest landscape undergoes natural processes with little human interference and, thus, provides a precious opportunity to study the natural processes shaping the forest landscape. The dynamics of fir forest in response to climate change has, however, not been well studied mainly due to hard accessibility to the remote forest area. Given that the climate will continue to change (Intergovernmental Panel on Climate Change 2007), it is pertinent to ask whether or not the forest will change its spatial structure and growth pattern. To answer this question, it requires knowledge about the ecological processes that regulates the forest dynamics.

The objectives of this study were (i) to examine the patterns in tree radial growth and recruitment in east Himalayan fir forest along an altitudinal gradient in the Mt. Everest region and (ii) to identify the climatic factors that are responsible to the observed patterns in forest growth and recruitment. The results obtained from this study will help clarify whether climatic factors or disturbances are influencing tree growth and recruitment on the Tibetan Plateau.

MATERIALS AND METHODS

Study area

This study was carried out in Dingjie County of the Mt. Everest Nature Reserve, southern Tibetan Plateau (Fig. 1). The study area (27°50′N, 87°27′E) is controlled by cold and snowy air masses from the north in winter and by warm and wet air masses from the Indian Ocean in summer. Based on instrumental records from 1967 to 2007 at weather stations in Dingri (28°38′N, 87°05′E, 4 300 m a.s.l.), Pali (27°44′N, 89°05′E, 4 300 m a.s.l.) and Nielamu (28°11′N, 85°58′E, 3 810 m a.s.l.) (Fig. 1), monthly mean air temperatures ranged from −6.6°C in January to 10.2°C in July and the annual mean value was 2.1°C. Forty-one-year mean annual total precipitation varies greatly among stations and ranged from 282 to 652 mm (Fig. 2a). Summer temperatures (June–September) during the last four decades showed obviously rising trends (Fig. 2b) while the precipitations of the three weather stations showed minor decreasing or no obvious trends (Fig. 2c).

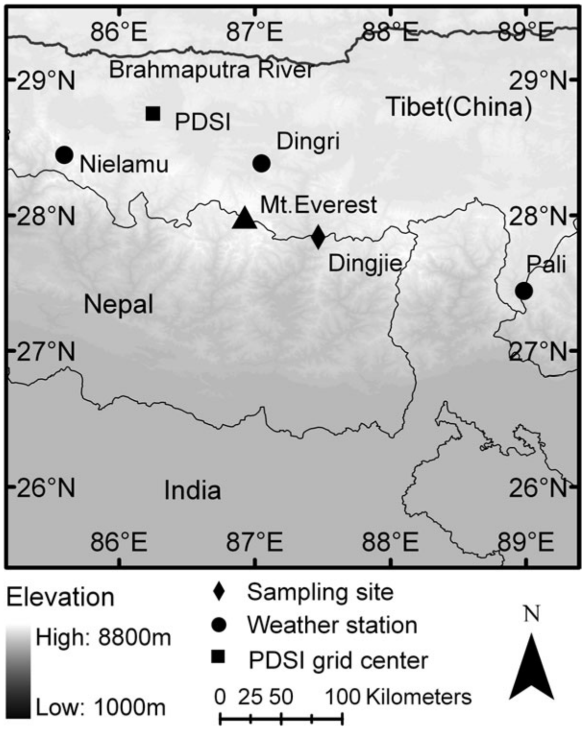

Figure 1: location of the study area in Dingjie of southern Tibet, China. The diamond represents the sampling site, solid circles represent weather stations and the solid square represents grid center of PDSI data (Dai *et al.* 2004). Lighter gray in the background represents higher elevation.

The study site was chosen in a continuous distribution of east Himalayan fir trees from the lower forest border (3 410 m) to the timberline (3 920 m). The fir tree is a canopy-dominant species. It possesses a single straight trunk with regularly spaced branch whorls produced at a rate of one whorl per year, so that it is sometimes possible to determine the age of a 50-year old tree simply by counting branch whorls (Xu 2001). Liang *et al.* (2011) found that counting the branch whorls may underestimate the true seedling age by up to 4 years after comparison with the fir seedling age obtained from the root collars in the field in southeastern Tibetan Plateau. Vegetation below the lower forest border was dense bamboo clusters and that above the timberline was *Rhododendron* clusters. In the lower part of the forest belt, firs co-dominated with *Betula utilis*, *Sorbus wallichii* and *Acer caudatum*, whereas in the upper part, firs formed a pure forest. There was little human interference with the forest because of the relatively sparse population in the region and the protection from the Mt. Everest Nature Reserve since the 1980s.

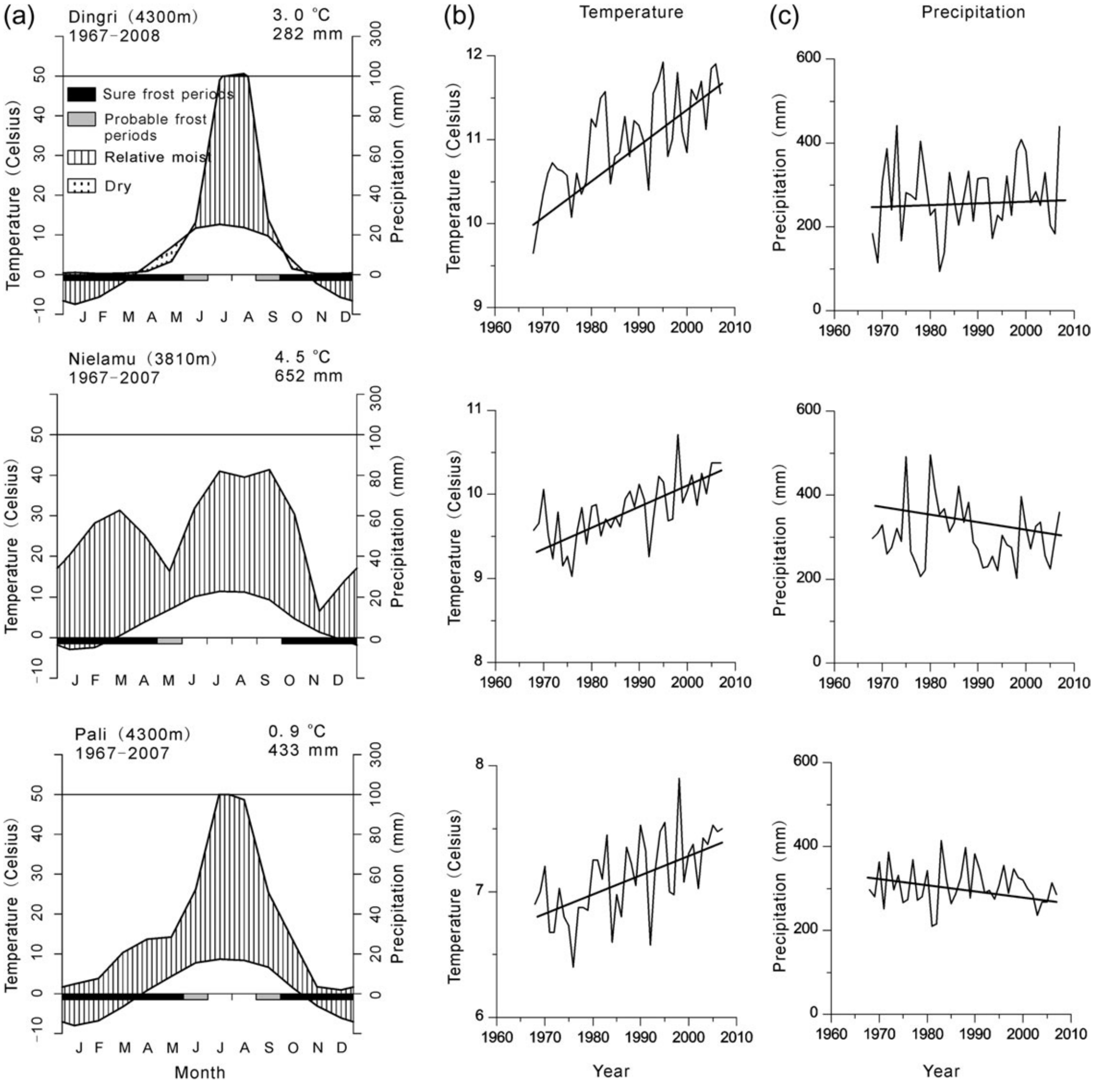

Figure 2: climate of the three weather stations near the sampling sites in Dingjie of the southern Tibet, China. (**a**) Climate diagrams, (**b**) temperatures in summer (June–September) and (**c**) precipitations in summer. The bold lines in (**b**) and (**c**) are long-term linear trends.

Plots and samples

In the summer of 2007, four sampling plots, each 60 m running up and down the slope and 30 m running along the elevation contour, were established along an altitudinal gradient from the lower to the upper limit of fir forest. They were named by the elevation at the upper line of each plot, i.e. Plots 3 410 m, 3 520 m, 3 700 m and 3 920 m (Table 1). These plots were selected with consideration of topography and forest structure that are similar to the forest at the corresponding elevation belt. Within each plot, all living trees were recorded in two- dimension coordinates. Tree diameters at breast height (DBH) were recorded except seedlings (height < 1.3 m) and saplings (DBH < 10 cm). For all adult firs, one core per tree was extracted in a direction parallel to the slope contour. An additional core from the opposite side was extracted if the increment core was broken. The age of fir seedlings and saplings was recorded by carefully counting the number of branch whorls and bud scars on the main stem. The age of young firs with a height just reaching the coring height (~1.3 m) were specifically selected to get knowledge of the time required for firs to grow to that height.

In total, 594 trees were surveyed within the four plots. There were 318 cores extracted from adult firs, 152 records of fir seedlings and saplings and 127 records of *B. utilis*, *S. wallichii*, *A. caudatum* and *Rhododendron arboreum*.

Age estimation

The increment cores were air-dried indoors, mounted on wooden slots and polished by progressively finer sandpaper till clear boundaries showed up. Tree-ring widths of these samples were measured to the nearest 0.001 mm using a TA Unislide Tree-Ring Measurement System (Velmex Inc., Bloomfield, NY). With the aid of a microscope, the tree rings were cross-dated by comparing the ring patterns among the samples, and the cross-dated tree-ring series were quality checked by the COFECHA program (Holmes 1983). Uncross-dated cores were excluded from chronology building.

For the cores that showed the pith, the tree age at the coring height was determined by counting the number of cross-dated tree rings (direct method). In cases where the pith was very close but not intercepted, 1–3 years were added for rings missing near the pith as judged by the curvature and widths of the innermost rings (curvature method) (Duncan 1989). For incomplete cores that did not show curvature in the innermost rings, the length of the missing radius was estimated by the distance to the geometric centre of the tree, and the age of the sample was obtained by extrapolating the mean growth rate of the 20 innermost rings in the cores (geometric centre method) (Norton *et al.* 1987; Rozas 2004). For the uncross-dated cores and incomplete cores that were less than a quarter of DBH in length, they were excluded from the analysis of age structure. Percentages of excluded trees in corresponding plots were calculated to evaluate the influence on the representativeness of the age structures.

The years required for firs growing from ground to the coring height, hereafter referred to as adjustment age, were estimated from the median value of the ages of young firs that have a coring height (125–135 cm). The age of each adult fir tree can then be obtained by adding adjustment age to the age at the coring height.

Following the age estimation procedures, 299 age estimates were processed into the final age structures while 14 fir trees were excluded (Table 2). The percentages of excluded fir trees ranged from 1.78% in Plot 3 410 m to 5.88% in Plot 3 920 m, indicating insignificant effect on the analysis of population dynamics.

Relationships between fir recruitment, growth and climate

Tree recruitment was studied by summarizing the age of firs in each plot into age distributions at 10-year intervals throughout the history. The time series of annually recruited fir seedlings and saplings were detrended by the best-fit trend functions, and the residuals were then normalized and averaged into 5-year classes to examine their correlations with the counterparts of the climate variables (a method similar to the one of Szeicz and Macdonald 1995).

Raw ring-width measurements were standardized and averaged to form a tree-ring standard chronology for each plot using the software ARSTAN (Cook 1985). Negative exponential or linear curves were fitted to the ring-width series to remove age and size-related growth trends. When the above functions failed to remove the trends, a smoothing spline function with 50% variance cutoff at half of the series length was used as an alternative function to detrend the series while retaining medium- to high-frequency growth signals (Cook and Peters 1981).

Meteorological records used for climate-growth analysis were obtained from the three nearest weather stations in the region (Fig. 1). The temperature from the Dingjie station which was the nearest to the sampling sites was used in the current study. The dataset covered a 48-year interval from 1959 to 2007. The precipitation varied greatly among the three stations (Fig. 2) and thus could not represent the precipitation regime of the study area. Instead of the precipitation, the monthly Palmer Drought Severity Index (PDSI) data (the grid cell is N27.5°–30.0°, E85.0°–87.5°, and the center point of which was shown in Fig. 1) from 1948 to 2004 was used to represent the moisture regime of the study area (Dai *et al.* 2004).

The relationships between tree-ring width standard chronology of each plot and monthly temperatures and monthly PDSIs were analyzed by response functions for the period 1959–2004 by using DendroClim2002 (Biondi and Waikul 2004). Because climate in the preceding growing season often influences tree growth of the following year (Fritts 1976), temperatures and PDSI data beginning in May of the previous growth year until September of the current growth year were used to analyze the relationship between annual radial growth and climate. Bootstrapping was used to test the significance of the response coefficients by examining the distribution of the coefficients calculated from a large number of subsamples randomly selected with replacement from the initial data set (1 000 replications in this study) (Biondi and Waikul 2004; Efron 1981). This method has advantages when the statistical properties of the data are not well understood.

Growth release analysis

To identify past disturbances that affected the canopy, a percentage growth change filter (Nowacki and Abrams 1997) was applied to tree-ring width sequences of 224 firs that were corssdated and reached pith (or absence of 1–3 years to pith). The formula used was as follows:

$$\%\mathrm{GC}_r = [M_2 - M_1)/M_1 \times 100,$$

where $\%\mathrm{GC}_r$ represented percentage of growth release and M_1 and M_2 were the preceding and subsequent 10-year ring-width means, respectively. The minimum threshold of 50% for $\%\mathrm{GC}_r$ was considered for release status recognition. A master growth-change chronology for each plot was built by averaging percentage growth change for all trees in each year. Stand-wide disturbance events were specifically denoted at peaks comprised of 25% of the sample trees (Nowacki and Abrams 1997). Probable release dates were further identified by abrupt change in annual growth rate with at least two standard errors. This cutoff has *a priori* probability of ~5%, a commonly used level of significant probability.

Running comparisons of sequential 10-year ring-width means were used to detect sustained growth increases indicative of canopy disturbance while discounting short-term climatic pulses and gradual ring-width changes due to tree aging, bole geometry and long-term climate shifts (Nowacki and Abrams 1997).

RESULTS

Plot information and size structure

Among the 152 fir seedlings and saplings, 139 were recorded from the timberline plot, and no fir seedlings or saplings were

Table 1: information about the fir plots in Dingjie of southern Tibet, China

Plot	3 920 m	3 700 m	3 520 m	3 410 m
Latitude	27°50.2′N	27°50.3′N	27°50.3′N	27°50.3′N
Longitude	87°28.2′E	87°27.8′E	87°27.6′E	87°27.4′E
Altitude (m)	3 887–3 918	3 657–3 698	3 478–3 518	3 378–3 408
Slope aspect	NW	N	N	NW
No. of adult fir trees	61	62	136	56
No. of fir seedlings and saplings	139	0	0	13
No. of other trees	1	19	63	44
No. stems/ha (≥10 cm DBH.)	344	450	1 106	556
Basal area of tree cover (%)	0.49	0.97	0.92	0.55

found in the two mid altitude plots (Table 1). The 127 records of trees from other species were mainly distributed in the two plots of lower altitude. The lowest stand density was 344 trees/ha in Plot 3 920 m and a roughly increase trend follows a downward elevation direction, with highest density reaching 1 106 trees/ha in Plot 3 520 m. Fir populations in the two medium plots have larger basal area of tree cover than those in the two border plots.

The adjustment age was 13 years (median value) for the plots at upper and lower altitudes, but the age range in the upper plot (10–20 years) was greater than that of the lower plot (10–14 years). This value of adjustment age was applied also in the two middle plots because no adequate saplings were available in these two plots. This age adjustment would result in an age bias of about 0–7 years, which can be removed dramatically by building the age structures in 10-year classes (Fig. 3). Mean ages of adult fir were 94, 130, 145 and 139 years for plots at 3 410 m, 3 520 m, 3 700 m and 3 920m. The oldest fir was 274 years old, which was found in Plot 3 700 m.

The DBH distribution in the timberline plot (Plot 3 920 m) displayed an ''L'' shape, whereas the other three plots showed a one-tailed bell shape (Fig. 4).

Pattern in fir recruitment

The frequency distribution of fir trees over time in the four plots showed that successful recruitment occurred in the years 1906–30 in Plot 3 410 m, the 1870–90 and the 1916–30 in Plot 3 520 m, the 1886–1910 in Plot 3 700 m and the 1976–2006 in Plot 3 920 m (Fig. 3).

In Plot 3 920 m, there were 72 fir seedlings and 67 fir saplings that occurred during the last three decades. Only 13 fir seedlings and saplings, including 4 emergences (sprouted within one growing season and considered as one-year old), were found in the Plot 3 410 m. There were no fir seedlings and saplings within the two plots at 3 520 and 3 700 m.

Fir recruitment and climate

In Plot 3 920 m (the timberline plot), fir recruitments in 5-year classes were positively correlated to their corresponding monthly mean air temperatures in June, July, August and September in the last four decades (Fig. 5a). Significant correlations were also found between fir recruitments in 5-year classes and their corresponding values of PDSI in June (Fig. 5b). The correlation coefficient of fir recruitment residuals (in 5-year classes) and seasonal air temperatures in June–September was 0.74 ($n = 7$, $P = 0.056$) (Fig. 6).

Table 2: number of trees of which the age was estimated by DM, CM and GCM and which were excluded from analyses (EC and %EC) due to poor sample quality for the four plots in Dingjie of southern Tibet, China

Plot	DM	CM	GCM	EC	%EC
3 920 m	36	18	7	3	4.69
3 700 m	30	25	5	2	3.22
3 520 m	89	23	16	8	5.88
3 410 m	39	15	1	1	1.78

Abbreviations: DM = direct method, CM = curvature method, GCM = geometric centre method, EC = exclusion

Fir radial growth and climate

The data from tree-ring measurements showed that the mean longevity of fir trees was greater in the upper two plots than that in the two lower plots while the mean radial growth rate did not show any altitudinal trend. The maximum fir radial growth rate was 8.64 mm at the 3 410-m plot, whereas it was 3.6 mm at the timberline plot. The mean intercorrelations of tree-ring sequences (R_{bar}) at the four plots were 0.233–0.267. The mean sensitivity did not show any regular trend along altitudinal gradients. The expressed population signal for each chronology was greater than 0.85 for the common period 1937–2006, indicating significant climate signals contained in the tree-ring chronologies (Table 3).

The standard tree-ring chronologies at the upper two plots showed similar variation in decadal scale with common periods of above-average growth occurring in the 1890s, 1930s and 1940s and below-average growth in the 1860–70 and 1960–90. The tree-ring chronologies at two lower plots showed a high similarity in interannual variation (Fig. 3).

Analysis of climate–tree growth relationship showed that tree-ring growth in the two upper plots was positively

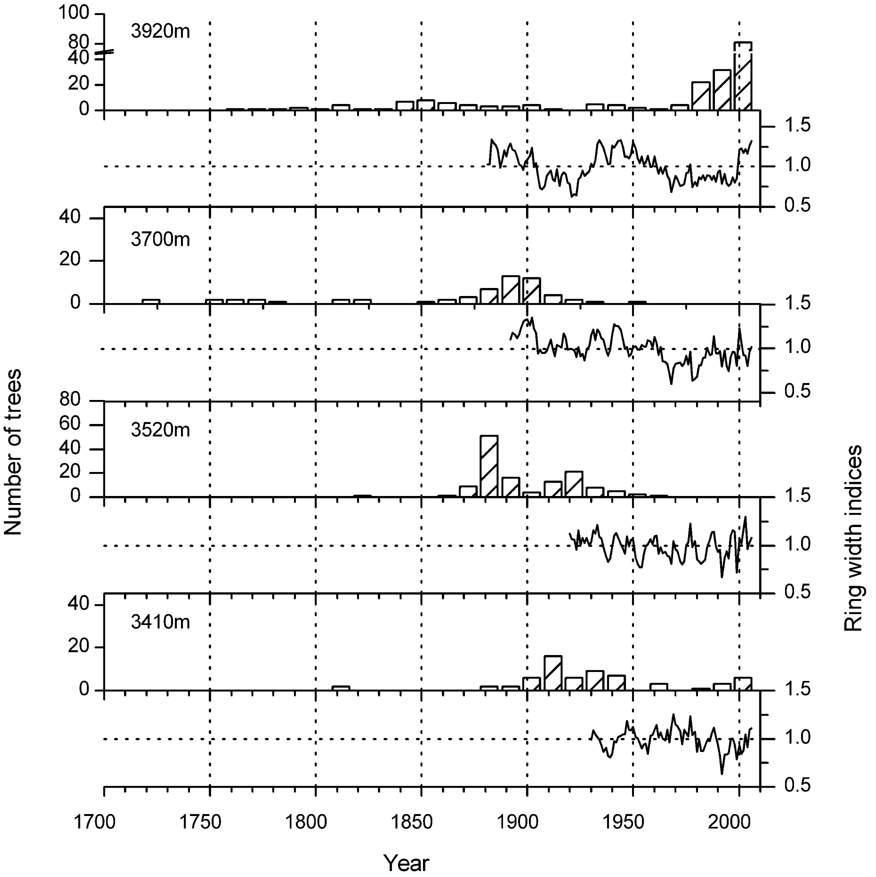

Figure 3: history of fir recruitment at the four plots and their corresponding standard tree-ring chronologies in Dingjie of southern Tibet, China. Numbers of fir recruitments are aligned into 10-year intervals and the standard chronologies are truncated to the years when expressed population signal >0.85.

correlated with early summer and winter temperature of the prior growth year and August temperature of the growth year and with PDSI in May to June of the growth year. Tree-ring growth in the two lower plots was positively correlated with PDSI from September of the prior growth year to the end of the current growth season (Fig. 7).

Growth release analysis and disturbance history

Growth change chronologies indicative of the disturbance history specific to each plot were developed (Fig. 8). Peaks of growth release occurred during 1820–40, 1870–1900, 1920–40 and 1970–90 in Plot 3 920 m, during 1820–30, 1870–90, 1930–40, 1950 and 1970–90 in Plot 3 700 m, during 1880, 1910 and 1970 in Plot 3 520 m and during 1900–10 and 1950–70 in Plot 3 410 m (Fig. 8a). Care should be taken to interpret release peaks when the sample replication became lower than five.

When the growth release events from all the individual trees were aligned to calendar 10-year intervals, it showed a temporal pattern similar to growth change chronology of the corresponding plot (Fig. 8b). In the strongest growth release event (in 1870–80) in Plot 3 920 m and 3 700 m, 60 and 41% of fir trees showed growth release signals.

DISCUSSION

Historical recruitments and disturbances

Forest stand size structure and static age structure are indicative of past disturbance patterns (Brown and Wu 2005; Cullen *et al.* 2001; Henry and Swan 1974; Hett and Loucks 1976). The typical ''L'' shape shown in the size structure of 10-cm DBH classes of all trees in Plot 3 920 m indicated an old growth forest with many young trees (Hörnberg *et al.* 1995). The irregular ''bell'' shapes in the size structure of other three plots indicated that the forests were characterized by one or several tree cohorts (Cullen *et al.* 2001). The static age structures showed that tree recruitment had a sporadic mode for 200 years (from 1760 to 1960) in Plot 3 920 m, whereas in the three lower plots it was characterized by an episodic mode with one or two peak periods. Both size and age structures suggested that disturbance was a main factor influencing the recruitment in all plots except Plot 3 920 m.

A severe disturbance occurred in 1870–80 across the whole elevational gradients (Fig. 8), and it might be a destructive one causing few surviving trees in the two lower elevational plots. The period 1864–78 was recorded as a drought epoch in instrumental records from Kathmandu in Nepal, south to this study

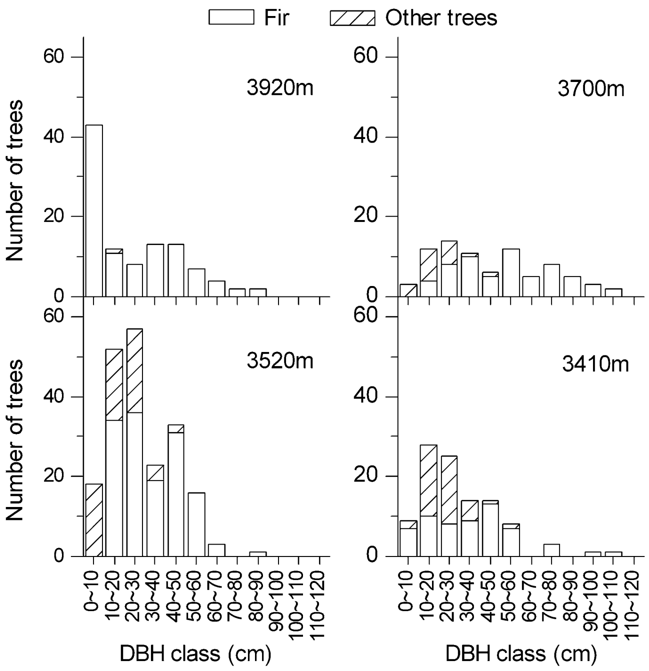

Figure 4: number of trees in 10-cm DBH classes in each plot in Dingjie of southern Tibet, China.

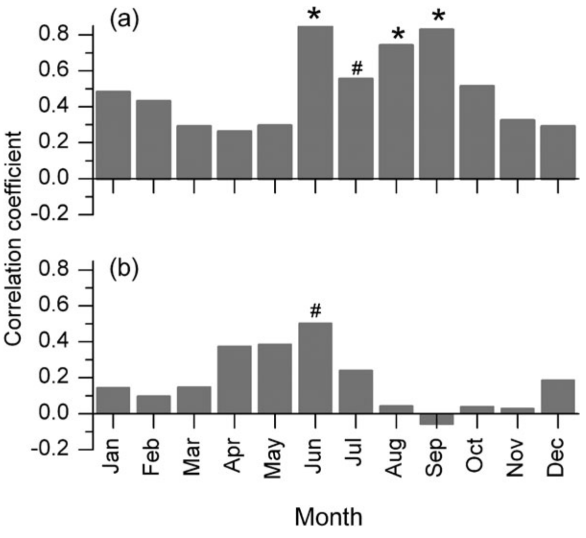

Figure 5: correlation coefficients between 5-year averaged fir recruitments at the timberline and monthly temperature from Dingri weather station (**a**) and the monthly Palmer Drought Severity Indices (PDSI) (**b**) for the period 1970–2004. Asterisks indicate significant at $P <$ 0.05 and # indicates significant at $P < 0.1$.

area (Cook *et al.* 2003). The period 1876–78 was also distinguished by a mega drought caused by Asian monsoon failure in recent research (Cook *et al.* 2010; Hao *et al.* 2010). Our study demonstrated that moisture availability is a factor limiting radial growth of fir trees in lower altitudes, which is consistent with the observation by Guarin and Taylor (2005).

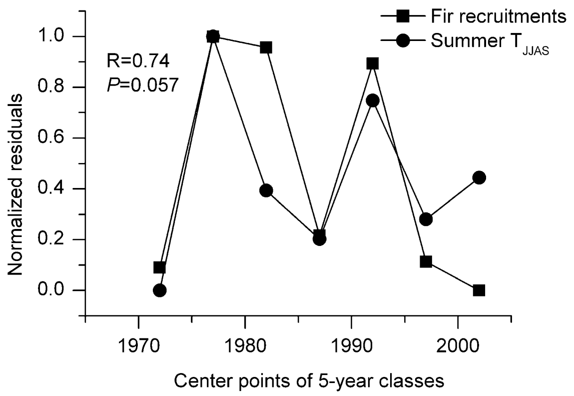

Figure 6: fir seedling and sapling recruitments averaged over 5-year intervals (residuals after removing trend) at timberline plot and the corresponding mean summer (June–September) temperatures at the Dingri weather station for the period 1970–2004.

Table 3: statistics of the four tree-ring residual chronologies developed from fir trees within the four plots in Dingjie of southern Tibet, China

Plot	Longest span (years)	MTRW ± SD (mm)	R_{bar}[a]	MS	EPS[a]
3 920 m	227	0.96 ± 0.466	0.267	0.122	0.933
3 700 m	234	1.75 ± 0.916	0.254	0.147	0.922
3 520 m	121	1.33 ± 0.799	0.241	0.120	0.943
3 410 m	114	1.85 ± 0.925	0.233	0.114	0.903

Abbreviations: MTRW = mean tree-ring widths, R_{bar} = mean correlation coefficients between tree-ring series, MS = mean sensitivity; EPS = expressed population signal.

[a] Calculated for the common period 1937–2006.

Massive canopy openings could provide space for tree recruitment (Sapkota and Odén 2009; Yamamoto 2000). The obvious recruitment in 1880–90 in the Plots 3 700 m and 3 520 m might be a result of canopy openings created by disturbance in 1870–80. The recruitment peak in 1900–10 in Plot 3,410 m might correspond to another standwide disturbance in 1906–07 as detected in Plot 3,520 and 3,410m (Fig. 8). This disturbance corresponded to a growth minimum in the standard chronology of Plot 3,520 m (Fig. 3), which is indicative of a drought condition. Comparing with Plot 3,700 m, the lag of fir recruitment in Plot 3,410 m by ~20 years suggested that the duration of drought in the lower forest limit was much longer.

No standwide disturbances were detected in the four plots after about the 1940s. Very limited fir trees recruited in Plot 3 700, 3 520 and 3 410 m. This phenomenon suggested that fir recruitment was more dependent on large-scale disturbance in lower altitude. Previous studies also reported that conifer regeneration in mixed forests depended on massive canopy mortality caused by great disturbance (Lusk and Smith 1998; Stueve *et al.* 2009) or long time drought depression (Guarin and Taylor 2005), especially at lower altitude.

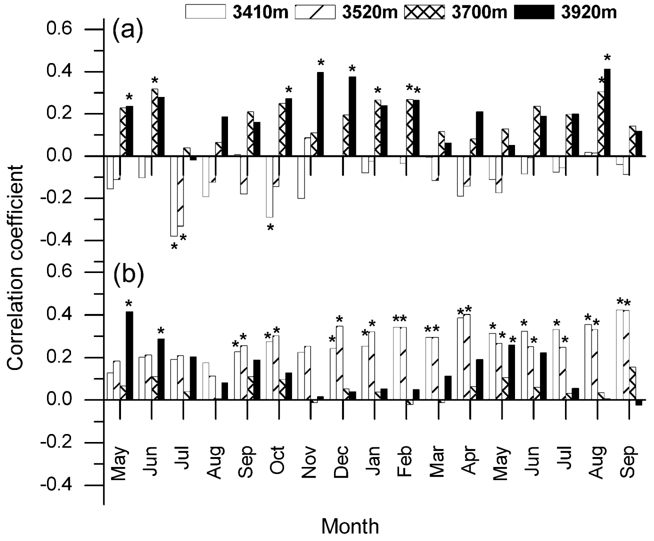

Figure 7: correlation coefficients between tree-ring chronologies of the four plots and monthly mean temperature from the Dingri weather stations (**a**) and monthly Palmer Drought Severity Indices (**b**). Asterisks indicate a 95% confidence level tested by bootstrap method.

In our comparison of historical tree recruitment and tree radial growth in the three lower plots, we found that most recruitment peaks roughly corresponded to several consecutive decades of above average tree-ring growth, but above average tree-ring growth was not necessarily accompanied by successful tree recruitment (Fig. 3). This suggests that the two processes were affected by similar climatic forces (Camarero and Gutiérrez 1999), but the climate was not the only decisive factor for recruitment. The asynchronous recruitment along altitudinal gradient suggests that habitat difference associated with altitude, e.g. disturbance, competition, as well as climate was in play and a more complex regeneration course existed in the forest at lower elevations than that at the timberline.

Factors affecting recent fir recruitment

The recent recruitment in the timberline plot was consistent with the Smith fir treeline on the SE Tibetan Plateau (Liang *et al.* 2011). It was found to have a positive correlation with mean summer air temperature (Fig. 5 & Fig. 6). Summer temperature in the study region ranged ~10–12°C, which is well below the optimum threshold ~20°C for photosynthesis (Grace *et al.* 2002). Higher photosynthesis rate under higher summer temperature could encourage both growth and nonstructural carbon storage, which is vital for fir seedlings to survive harsh winter climate (Camarero and Gutiérrez 1999). Previous observation also suggested that viable seed at high elevation would not have high production except in exceptionally warm years (Barclay and Crawford 1984; Millar and Cummins 1982; Tranquillini 1979). Summer temperature limitation on forest regeneration were also reported from Scotch pine forest in northern Europe (Hustich 1958), from conifer seedlings in alpine treeline ecotone of the Snowy Range in Wyoming, USA (Germino and Smith 1999), from spruce (*P. schrenkiana*) forest in central Tianshan Mountains, northwestern China (Wang *et al.* 2006) and from a multispecies study in subarctic area (Danby and Hik 2007).

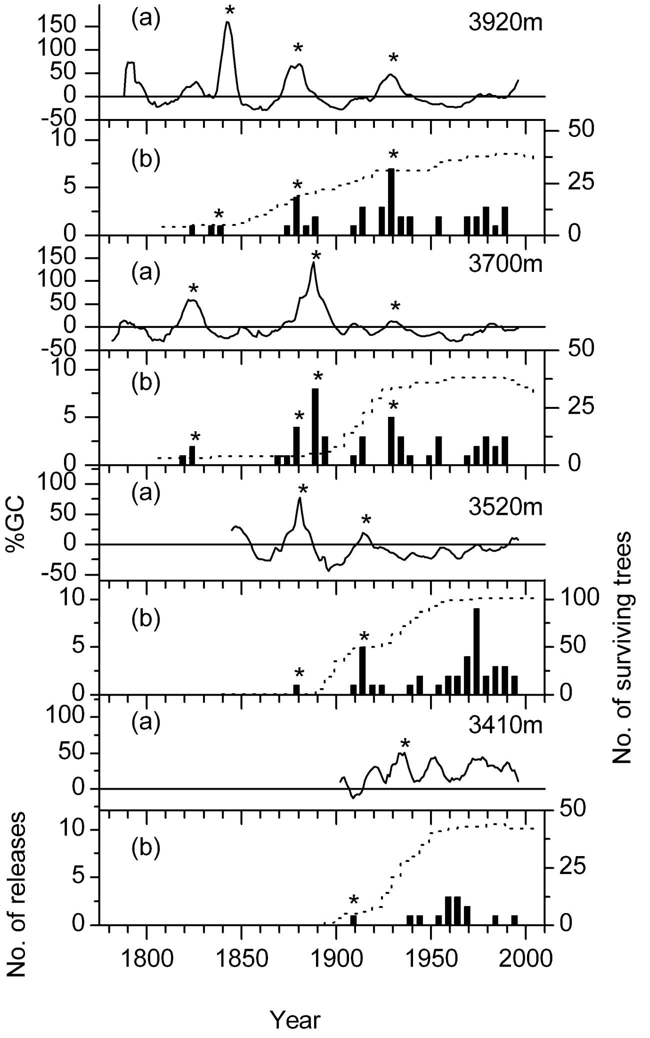

Figure 8: growth release analysis for the four altitudinal plots of fir forest in Dingjie of Southern Tibet, China. (**a**) Percent of growth change (%GC) chronology at annual scale; (**b**) number of trees showing release in corresponding 10-year intervals as indicated by bars and the number of surviving trees as indicated by broken lines. Asterisks indicate growth release peaks.

In the three lower plots, there were no obvious recruitments in the past several decades. A difference between the three lower plots and the timberline plot (Plot 3 918 m) was species composition, i.e. the timberline plot was a pure fir forest, whereas the three lower plots were mixed with broadleaf species. The coverage of herbaceous layer in these plots also increased with the decrease in elevation. The competition for space and nutrients from other species could be a factor inhibiting recruitment of fir trees in the three lower plots, which is consistent with observations in other studies (George and Bazzaz 1999; Gobbia and Schlichter 1998; Kunstler *et al.* 2011).

In conclusion, our study provided a two-century long tree-ring growth and recruitment history of an east Himalayan fir forest along altitudinal gradient in Mt. Everest Nature Reserve. Our results implies that if the association between timberline forest regeneration and summer temperature holds in future, the forest stand at the timberline will probably be more dense under continued global warming. In the meantime, if higher temperature increases moisture stress in the lower altitudinal sites, the forest will be vulnerable to drought-related disturbances as happened in the history. Our results provide a reference line for predicting future forest landscape in the Mt. Everest Nature Reserve and similar alpine environments.

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REFERENCES

Abrams MD, Ruffner CM, DeMeo TE (1998) Dendroecology and species co-existence in an old-growth *Quercus-Acer-Tilia* talus slpoe forest in the central Appalachians. *USA For Ecol Manage* **106**:9–18.

Barclay AM, Crawford RMM (1984) Seedling emergence in the rowan (*Sorbus aucuparia*) from an altitudinal gradient. *J Ecol* **72**:627–36.

Biondi F, Waikul K (2004) Dendroclim2002: A c++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput Geosci* **30**:301–11.

Brown PM, Wu R (2005) Climate and disturbance forcing of epicosic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* **86**:3030–8.

Camarero JJ, Gutiérrez E (1999) Structure and recent recruitment at alpine forest–pasture ecotones in the Spanish central Pyrenees. *Ecoscience* **6**:451–64.

Camareno JJ, Gutiérrez E (2004) Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees. *Climat Change* **63**:181–200.

Cook ER (1985) A Time Series Analysis Approach to Tree-Ring Standardization. *Dissertation*. University of Arizona:.

Cook ER, Anchukaitis KJ, Buckley BM, *et al.* (2010) Asian monsoon failure and megadrought during the last millennium. *Science* **328**:486–9.

Cook ER, Krusic PJ, Jones PD (2003) Dendroclimatic signals in long tree-ring chronologies from the Himalayas of Nepal. *Int J Climatol* **23**:707–32.

Cook ER, Peters K (1981) The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull* **41**:45–53.

Cuevas JG (2002) Episodic regeneration at the *Northofagus pumilio* alpine timberline in tierra, Chile. *J Ecol* **90**:52–60.

Cullen LE, Stewart GH, Duncan RP, *et al.* (2001) Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *J Ecol* **89**:1061–71.

Dai AG, Trenberth KE, Qian T (2004) A global dataset of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *J Hydrometeorol* **5**:1117–30.

Dalen L, Hofgaard A (2005) Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, Alpine Res* **37**:284–96.

Danby RK, Hik DS (2007) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *J Ecol* **95**:352–63.

Duncan RP (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Nat Sci* **16**:31–7.

Efron B (1981) Nonparametric estimates of standard error: the jackknife, the bootstrap and other methods. *Biometrika* **68**:589–99.

Fritts HC (1976) Tree Rings and Climate. London: Academic Press.

George LO, Bazzaz FA (1999) The fern undersroty as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology* **80**:846–56.

Germino MJ, Smith WK (1999) Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell Environ* **22**:407–15.

Germino MJ, Smith WK, Resor AC (2002) Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecol* **162**:157–68.

Gobbia M, Schlichter T (1998) Survival of *Austrocedrus chilensis* seedlings in relation to microsite conditions and forest thinning. *Forest Ecol Manage* **111**:137–46.

Grace J, Berninger F, Nagy L (2002) Impacts of climate change on the tree line. *Ann Bot* **90**:537–44.

Guarin A, Taylor AH (2005) Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *For Ecol Manage* **218**:229–44.

Gutiérrez A, Barbosa O, Christie D, *et al.* (2008) Regeneration patterns and persistence of the fog dependent Fray Jorge forest in semiarid Chile during the past two centuries. *Global Change Biol* **14**:161–76.

Hörnberg G, Ohlson M, Zackrisson O (1995) Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth *Picea abies* swamp-forests. *J Veg Sci* **6**:291–8.

Hao Z, Zheng J, Wu GF, *et al.* (2010) 1876–1878 severe drought in north China: facts, impacts and climatic background. *Chinese Sci Bull* **55**:3001–7.

Henry JD, Swan JMA (1974) Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. *Ecology* **55**:772–83.

Hett JM, Loucks OL (1976) Age structure models of balsam fir and eastern hemlock. *J Ecol* **64**:1029–44.

Holmes RL (1983) Computer-assisted quality control in tree-ring data and measurement. *Tree-Ring Bull* **43**:69–78.

Hustich I (1958) On the recent expansion of the scotch pine in northern Europe. *Fennia* **82**:1–25.

Intergovernmental Panel on Climate Change (2007) Climate Change 2007: The Physical Science Basis. In Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.). *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Kullman L (1987) Long-term dynamics of high altitude populations of *Pinus sylvestris* in the Swedish Scandes. *J Biogeogr* **14**:1–8.

Kullman L (1993) Tree limit dynamics of *Betula pubescens* ssp. *tortuosa* in relation to climate change variability: evidence from central Sweden. *J Veg Sci* **4**:765–72.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol* **90**:68–76.

Kunstler G, Albert CH, Courbaud B, *et al.* (2011) Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *J Ecol* **99**:300–12.

Liang E, Wang Y, Eckstein D, *et al.* (2011) Little change in the fir treeline position on the southeastern tibetan plateau after 200 years of warming. *New Phytol* **190**:760–9.

Lusk CH, Smith B (1998) Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* **79**:795–806.

Millar GR, Cummins RT (1982) Regeneration of scots pine (*Pinus sylvestris*) at the natural treeline in the Cairgorm Mountains, Scotland. *Holartic Ecol* **5**:27–34.

Norton DA, Palmer JG, Ogden J (1987) Dendroecological studies in New Zealand. 1. An evaluation of age estimates based on increment cores. *N Z J Bot* **25**:373–83.

Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol Monogr* **67**:225–49.

Rozas V (2004) A dendroecological reconstruction of age structure and past management in an old-growth pollarded parkland in northern Spain. *For Ecol Manage* **195**:205–19.

Sapkota IP, Odén PC (2009) Gap characteristics and their effects on regeneration, dominance and early growth of woody species. *J Plant Ecol* **2**:21–9.

Stueve KM, Cerney DL, Rochefort RM, *et al.* (2009) Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA. *J Veg Sci* **20**:107–20.

Szeicz JM, Macdonald GM (1995) Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *J Ecol* **83**:873–85.

Tranquillini W (1979) Physiological Ecology of the Alpine Treeline. Berlin, Germany: Springer.

Veblen TT, Hadley KS, Nel EM, *et al.* (1994) Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J Ecol* **82**:125–35.

Wang T, Zhang Q-B, Ma K (2006) Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Global Ecol Biogeogr* **15**:406–15.

Xu LX (2001) Ecology Episode of Xi Zang in the Last 50 Years. Beijing, China: National Publishing House (in Chinese).

Yamamoto S-I (2000) Forest gap dynamics and tree regeneration. *J For Res* **5**:223–9.