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RESEARCH PAPER

Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China

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ABSTRACT

Aim Climate variability may be an important mediating agent of ecosystem dynamics in cold, arid regions such as the central Tianshan Mountains, northwestern China. Tree-ring chronologies and the age structure of a Schrenk spruce (*Picea schrenkiana*) forest were developed to examine treeline dynamics in recent decades in relation to climatic variability. Of particular interest was whether tree-ring growth and population recruitment patterns responded similarly to climate warming.

Location The study was conducted in eight stands that ranged from 2500 m to 2750 m a.s.l. near the treeline in the Tianchi Nature Reserve (43°45′–43°59′ N, 88°00′–88°20′ E) in the central Xinjiang Uygur Autonomous Region, northwestern China.

Methods Tree-ring cores were collected and used to develop tree-ring chronologies. The age of sampled trees was determined from basal cores sampled as close as possible to the ground. Population age structure and recruitment information were obtained using an age–d.b.h. (diameter at breast height) regression from the sampled cores and the d.b.h. measured on all trees in the plots. Ring-width chronologies and tree age structure were both used to investigate the relationship between treeline dynamics and climate change.

Results Comparisons with the climatic records showed that both the radial growth of trees and tree recruitment were influenced positively by temperature and precipitation in the cold high treeline zone, but the patterns of their responses differed. The annual variation in tree rings could be explained largely by the average monthly minimum temperatures during February and August of the current year and by the monthly precipitation of the previous August and January, which had a significant and positive effect on tree radial growth. *P. schrenkiana* recruitment was influenced mainly by consecutive years of high minimum summer temperatures and high precipitation during spring. Over the last several decades, the treeline did not show an obvious upward shift and new recruitment was rare. Some trees had established at the treeline at least 200 years ago. Recruitment increased until the early 20th century (1910s) but then decreased with poor recruitment over the past several decades (1950–2000).

Main conclusions There were strong associations between climatic change and ring-width patterns, and with recruitments in Schrenk spruce. Average minimum temperatures in February and August, and total precipitation in the previous August and January, had a positive effect on tree-ring width, and several consecutive years of high minimum summer temperature and spring precipitation was a main factor favouring the establishment of *P. schrenkiana* following germination within the treeline ecotone. Both dendroclimatology and recruitment analysis were useful and compatible to understand and reconstruct treeline dynamics in the central Tianshan Mountains.

Keywords

Age structure, climatic fluctuation, *Picea schrenkiana*, radial growth, treeline dynamics, tree rings.

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INTRODUCTION

The average temperature at the Earth's surface has increased by approximately 0.8 °C from 1866 to 1998 (Bluemle, 1999), and global temperatures are predicted to rise an additional 1.5–4.5 °C by AD 2100 (Houghton *et al*., 1996). Treeline ecotones are sensitive biomonitors of past and recent climate change and variability (Kullman, 1998; Camarero & Gutiérrez, 2004) and have received much attention in recent decades. Much treeline research has focused on the relationships between vegetation and climate by examining two major aspects: tree rings and age structure. The strongest relationships between tree radial growth and climatic factors are often found at natural latitudinal (Briffa *et al*., 1995; Cullen *et al*., 2001) and altitudinal treelines (Villalba *et al*., 1997; Cullen *et al*., 2001), and this is used widely as a proxy for reconstructing past climates (Fritts, 1976; Bradley & Jones, 1992). In addition, other studies on treeline dynamics have shown that population structures at treeline ecotones are good indicators of climate change (Payette & Filion, 1985; Szeicz & MacDonald, 1995; Weisberg & Baker, 1995), where trees often respond to climatic warming (Payette & Filion, 1985; Lloyd & Graumlich, 1997) with increases in recruitment (Kullman, 1986, 1990; Payette & Lavoie, 1994) or tree-density (e.g. Szeicz & MacDonald, 1995; Camarero & Gutiérrez, 2004), as well as upward advances in the treeline (Bradley & Jones, 1993; Camarero & Gutiérrez, 2004).

It has been suggested that dendroclimatic data alone cannot determine the causes of changes in the structure of ecosystems and populations (Moiseev, 2002). In fact, both processes are interrelated and help to understand treeline dynamics. For example, it has been shown that studying tree-ring chronologies coupled with stand age structures, climatic data and ecological attributes of individual species is a particularly strong approach for understanding long-term forest dynamics (Abrams *et al*., 1998; Ruffner & Abrams, 1998). For mature long-lived tree populations, the static age structure (the distribution and range of tree ages) of living trees represents the change in the rate of tree recruitment and mortality over time (Harcombe, 1987), and a static investigation of the age structure of a stand is often considered as a means for understanding tree population dynamics (Stewart, 1986; Johnson & Fryer, 1989; Svensson & Jeglum, 2001). Tree populations at their distributional margins are theoretically very sensitive to climate variability (Brubaker, 1986). It has almost become axiomatic that climate exerts primary control over latitudinal and elevational tree limits and that treeline dynamics accurately reflect climatic fluctuations and change (Brubaker, 1986). However, we still do not know how climate affects the recruitment and growth of many treeline species at different sites. Moreover, these two processes may respond differently to climatic factors (Earle, 1993).

Although some dendrochronological studies have been conducted in the central Tianshan Mountains, north-western China (e.g. Yuan & Li, 1999; Yuan *et al*., 2001), little is known of recent alpine treeline dynamics. The present study focuses on the upper treeline ecotone of a *Picea schrenkiana* forest to examine treeline dynamics in recent decades by evaluating the sensitivity of tree rings and stand recruitment to climatic variations. Of particular interest was whether tree-ring growth and population recruitment patterns responded similarly to climate warming.

METHODS

Study area and site selection

This study was conducted in the Tianchi Nature Reserve (43°45′ 43°59′ N–88°00′–88°20′ E) in the central Xinjiang Uygur Autonomous Region, north-western China. The nearest weather station to our sampling sites is the Tianchi meteorological station (1935 m a.s.l., 43°53′ N, 88°07′ E), which is less than 1 km from all our sampling sites. The mean annual total precipitation is 400–500 mm and the mean annual temperature is 2.04 °C. The mean annual nonfrost period is 88.6 days, and the mean relative humidity is 56–64%.

Schrenk spruce, *P. schrenkiana* (Fisch. et Mey.), is the dominant tree species in the central Tianshan Mountains forming single-species stands (Zhang & Tang, 1989) between approximately 1500 and 2700 m a.s.l. This forest is part of the National Nature Reserve and generally is well protected. The uppermost trees are often situated in fairly inaccessible places and at low densities which has resulted in very little disturbance by humans, pathogens or animals. No evidence of fire or previous logging was found in the treeline stands, but some dead fallen decomposed trees were evident (Table 1). *P. schrenkiana* is found only on mesic north-facing slopes; their growth and reproduction patterns are similar in the same altitudinal stands, especially in the high altitudinal treeline. We selected typical stands in the upper treeline zone that had similar topography and avoided wet microsites or rock outcrops (Wang *et al*., 2004).

Some broad-leaved trees and shrubs, e.g. *Sorbus tianschanica* Rupr., *Salix xerophila* Flod., *Betula tianschanica* Rupr., *B. verrucosa* Ehrh. and *B. microphylla* Bunge, are found in the forest. There is also a dense understorey of *Sabina pseudosabina* (Fisch. et May) Cheng et W. T. Wang, which increases with increasing altitude in the treeline zone (Table 1). The soil of the study site was classified as a mountain grey-brown forest soil type (Zhang & Tang, 1989).

Field sampling

The field investigation was carried out from June 1 to August 6, 2002. Plots were selected at 100-m elevation intervals from 2500 m to 2700 m a.s.l., and two plots (20 × 20 m) were established at each elevation. The stands at 2750 m a.s.l. zone may be the highest altitudinal limits of *P. schrenkiana* as there are only a few trees. Accordingly, two plots were also established at 2750 m a.s.l.; however, only a few trees were present in one of the plots and the second plot was dominated by *S. pseudosabina*, with only a single *P. schrenkiana* tree. In total, eight plots (20 × 20 m) were established in the treeline zone that ranged from 2500 m to 2750 m a.s.l. (Fig. 1).

Table 1 Stand characteristics of different sites along the treeline ecotone

	Coverage of different layers (%)		Stem density per 1000 m^2			
Altitude of plots (m a.s.l)	*Picea schrenkiana*	*Sabina pseudosabina*	Seedlings (< 0.5 m high)	Saplings (0.5–2 m high)	Living trees (> 2 m high)	Fallen trees
2800	0	98.5% ± 1.4%	0	0	0	0
2750	11.9% ± 1.6%	95.7% ± 2.5%	0	1 ± 1	8 ± 3	0
2700	30.8% ± 5.4%	64.6% ± 5.6%	6 ± 3	14 ± 6	40 ± 8	6 ± 6
2600	55.3% ± 24.6%	13.3% ± 4.9%	3 ± 1	8 ± 3	88 ± 8	26 ± 4
2500	59.3% ± 13.2%	1.8% ± 1.6%	4 ± 2	5 ± 1	119 ± 23	69 ± 21

*Data are presented in mean ± SE.

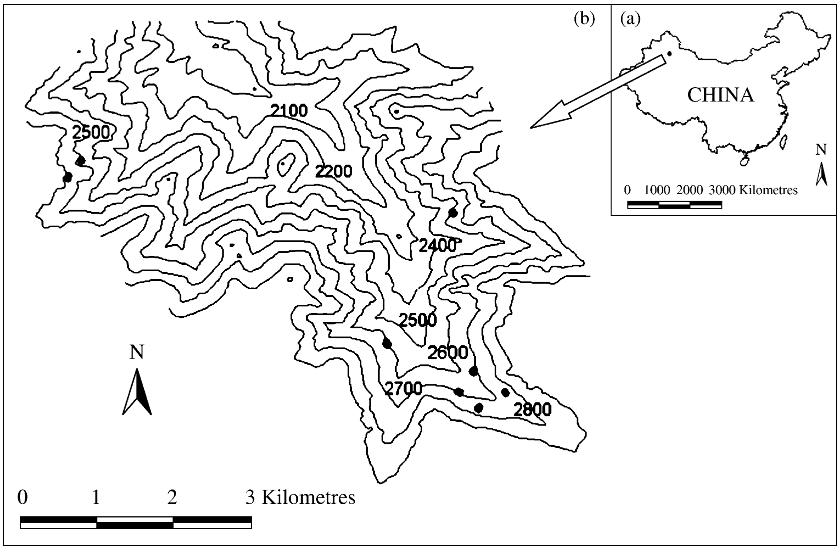

Figure 1 Location of plots in the treeline zone of Tianshan Mountains, northwestern China. (a) Location of the study area in China. (b) Scheme of plots (2500–2750 m a.s.l) in Tianchi Nature Reserve (88°00′–88°20′ E, 43°45′–43°59′ N) in the central Xinjiang Uygur Autonomous Region.

In each plot, *P. schrenkiana* individuals were enumerated into three height classes: trees (> 2 m), saplings (0.5–2 m) and seedlings (< 0.5 m). The d.b.h. (diameter at breast height) of each tree was measured and all trees were grouped into 5-cm diameter interval size classes in every plot. At least two trees per d.b.h. class and two cores per tree were selected randomly in each plot and cored as close to the ground as possible to establish age–d.b.h. relationships. Also, some trees were sampled for developing a chronology following standard dendrochronological techniques, taking at least two cores per tree at a height of 1.3 m. In addition, the age of seedlings and saplings was determined by counting the number of branch whorls and bud scars on the main stem.

Chronology development and dendroclimatic analysis

All cores were mounted and sanded with successively finer grades of sandpaper until annual rings could be distinguished easily. The rings were counted and ring widths measured to the nearest 0.001 mm using WinDENDROTM 2001b (Université Du Québec À Chicoutimi, Canada). All measured ring-width sequences were plotted, and the patterns of wide and narrow rings were cross-dated among trees to identify possible false rings, missing rings or measurement mistakes. The quality of cross-dating was examined using the software COFECHA (Holmes, 1983), which provides clues of the best match for ring patterns by calculating correlation coefficients among tree-ring sequences. Some cores were discarded because of missing rings or rot in the centre and only those cores that passed through the centre of the tree were used in further analysis. In total, 73 cores from 40 trees were used to form the chronology for the high treeline site.

Detrending of each tree-ring series, i.e. the removal of the natural decrease in ring-widths as the tree ages, was accomplished using the program ARSTAN (Cook, 1985), and either negative exponential curves or straight lines with a negative or horizontal slope were used to remove natural growth trends (Fritts, 1976; Szeicz & MacDonald, 1994). By using the ARSTAN program, a residual chronology that contained only high-frequency variation was developed to maximize the climatic signal. The quality of the chronology was assessed on the basis of the following statistical parameters: standard deviation (SD), mean sensitivity (MS), signal to noise ratio (SNR) and expressed population signal (EPS).

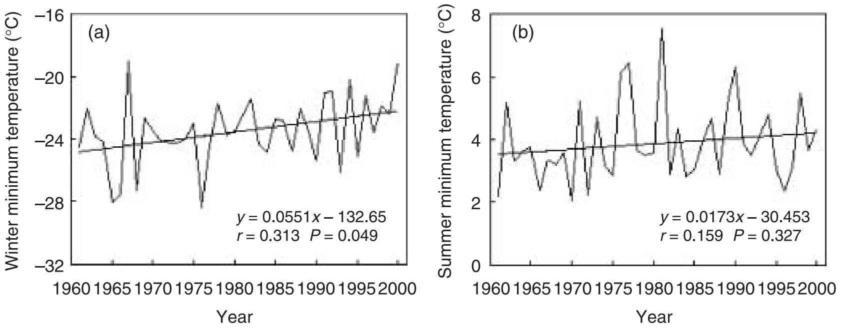

Figure 2 Variation in (a) winter minimum temperatures (December–February) and (b) summer minimum temperatures (June–August) for the period 1961–2000 based on observed data from the Tianchi meterological station (1935 m a.s.l).

In this study, correlation coefficients were used to quantify relationships between tree-ring chronologies and two climate variables, mean monthly minimum temperature and total monthly precipitation (Fritts, 1976; Cook & Kairiukstis, 1990; Tardif & Conciatori, 2001) using PRECONK software version 5.17 (Fritts, 1998). Because climate in the preceding growing season often influences tree growth the following year (Fritts, 1976; Yadav & Singh, 2002), temperature and precipitation data beginning in June of the previous growth year until August of the current growth year from the Tianchi meteorological station (1961–2000) were used to analyse the relationship between annual radial growth and climate.

Age structure and establishment analysis

A regression model of tree d.b.h and age was developed to estimate the ages of all trees in each plot, in which the ages from 48 sampled trees were used to form the age–d.b.h. regression model for the high treeline site. However, this ageing method, as well as the methodology used to determine the age of seedlings and saplings, may underestimate age by 0–5 years, which can be removed partially by showing the age structure in 5-year classes (Kullman, 1983; Camarero & Gutiérrez, 1999). To investigate the relationship between establishment and climate change, recruitment from 1961 to 2000 was summed across 5-year intervals and compared with monthly and seasonal climate records compiled into 5-year averages over the same time period (Camarero & Gutiérrez, 1999). The climate parameters used in the analyses include mean monthly minimum temperatures and monthly total precipitation.

RESULTS

Local climate trends and stand characteristics

Weather data from the Tianchi meteorological station showed that the trends of summer (June–August) and winter (December –February) temperatures were very different over time (1961–2000) (Fig. 2a,b). Between 1961 and 2000, the winter minimum temperature showed an average increase at a rate of 0.055 °C per year ($r = 0.313$, $P = 0.049$), whereas mean summer temperatures decreased slightly at a rate of 0.002 °C per year ($r = 0.032$, $P = 0.845$).

P. schrenkiana trees and *S. pseudosabina* shrubs are the two major species that coexist at the high treeline zone. The coverage of *P. schrenkiana* and *S. pseudosabina* changed with elevation upslope, whereas the density of *P. schrenkiana* (including seedlings, saplings, living trees and fallen trees) did not appear to change dramatically with increasing altitude. Moreover, it is noteworthy that seedlings and saplings of *P. schrenkiana* were very rare in the upper treeline zone (Table 1).

Chronology and descriptive statistics

The ring-width measurements of the *P. schrenkiana* series have been used to develop a 280-year (AD 1721–2000) ring-width residual chronology (Fig. 3b). During the twentieth century tree-ring width indices increased over time with a peak in 1952, decreased during the following several years (1953–59), and has been rising and maintaining a steady increase until recent years (Fig. 3b). The residual chronology exhibited interannual variation with a mean sensitivity of 0.151, and a standard deviation of 0.156. The common interval statistics, such as signal-to-noise ratio (21.166) and total variance explained in the first eigenvector (47.97%) suggest suitability of the Schrenk spruce chronology for climatic studies (Table 2).

Radial growth trends with climate

The correlation analysis showed that radial growth was significantly and positively correlated with mean minimum temperatures for February ($r = 0.312$, $P < 0.05$) and August ($r = 0.34$, $P < 0.05$) (Fig. 4a). A negative correlation, although not significant, was also found with mean minimum temperatures during April, May and July. Rainfall appeared to be another important growth-limiting factor in these arid mountains. Rainfall in both August ($r = 0.45$, $P < 0.05$) of the previous year and January ($r = 0.332$, $P < 0.05$) of the current year correlated significantly with the current radial growth (Fig. 4a). Precipitation of the previous December and precipitation during April and July of the current year were also correlated positively with tree growth, although not significantly.

Distribution of d.b.h. and age structure

The Schrenk spruce population showed a bell-shaped size distribution pattern (5-cm d.b.h. classes), and individuals in the < 5 cm, 10–15 cm and ≥ 45 cm d.b.h. size classes accounted for 4.46%, 24.75% and 2.97% of the total stems, respectively

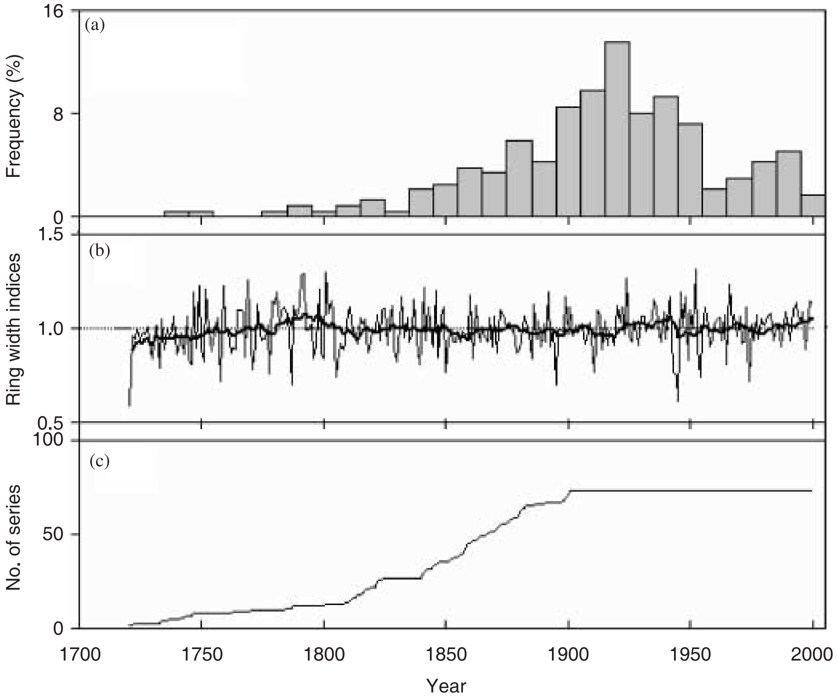

Figure 3 Age structure and radial growth patterns of a *Picea schreckiana* population at the treeline ecotone in the central Tianshan Mountains. (a) Age structure of 242 trees from eight plots (20×20 m^2) at treeline. The first bar at year 1940 gives the distribution percentage in the 1731–1740 age class, the second bar at year 1750 gives the 1741–1750 age class, and so on. (b) Ring-width indices: annual series (thin line) and 10-year smoothing spline superimposed on the annual values (thick line). (c) The number of cores included in the residual chronology.

Table 2 General statistics for residual chronology of *Picea schrenkiana* at the treeline zone of the Tianshan Mountains

Chronology length	1721–2000
Number of cores/trees	73/40
Mean	0.991
MS (mean sensitivity)	0.151
SD (standard deviation)	0.156
AC1 (autocorrelation order 1)	0.069
Common interval time span	1882–2000
Number of cores/trees	68/38
Mean correlations:	
Among all radii	0.361
Between trees	0.358
Within trees	0.616
Signal-to-noise ratio (SNR)	21.166
Express population signal (EPS)	0.955
Variance in first eigenvector (%)	47.97

(Fig. 5). The correlation between age and d.b.h. of trees was statistically significant ($n = 48$, $r = 0.848$, $P < 0.001$) (Fig. 6), and this relationship was used to estimate the age of all trees.

Similar to the d.b.h. frequency distribution (5-cm d.b.h. classes), the age–frequency of *P. schrenkiana* also displayed a bell-shaped distribution (10-year intervals) (Fig. 3a). The 81–90-year-old age class (trees that established in the 1910s) accounted for the largest age class (13.6%). The majority of trees (66.8%) were between 51 and 130 years old, which successfully established between 1870 and the 1940s. However, in recent decades (1951–2000), establishment has been very poor with young individuals (< 50 years) accounting for only 16.2% of the total population.

Recent regeneration and climate

Age-class histograms for *P. schrenkiana* showed that trees could be dated back to the early eighteenth century. Establishment in this population occurred at low levels before 1830, at moderate levels from 1830 to 1890, and at high levels between 1890 and the 1940s, but regeneration has declined substantially since the 1950s (Fig. 3a). During the last 40 years, there have been significant and positive correlations between recruitment and total precipitation (5-year average) for June ($r = 0.629$, $P = 0.094$) and spring ($r = 0.766$, $P = 0.027$), and significant negative correlations with total monthly precipitation for March ($r = -0.727$, $P = 0.041$) and August ($r = -0.655$, $P = 0.078$) (Fig. 4b). High minimum monthly temperatures from May to late autumn (October) also favoured *P. schrenkiana* recruitment. We found the highest significant and positive correlations between recruitment and mean summer minimum temperature ($r = 0.646$, $P = 0.084$).

DISCUSSION

Radial growth and climate correlations

High correlations among *P. schrenkiana* individuals that formed the residual chronology showed a synchronicity in their inter-annual variation in ring-width patterns. High SNR and EPS, as well as a relatively high percentage of the variance, accounted for by the first principal component of the tree-ring indices, indicated that all trees shared a strong regional common signal. Furthermore, the mean sensitivity of the chronology for this Schrenk spruce stand was 0.151, which was high enough to obtain accurate results with correlation function methods (Rolland, 1993). Statistical characteristics of the chronology

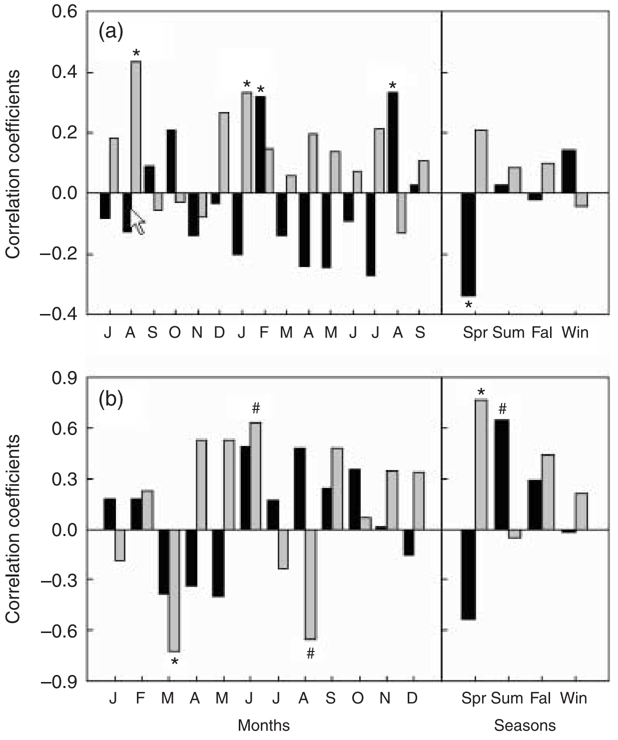

Figure 4 Correlations between climate change and ring-width indices and recruitments of a *Picea schreckiana* population at treeline in the central Tianshan Mountains. (a) Correlation coefficients of the residual chronology with monthly or seasonal minimum temperatures and monthly total precipitation (1961–2000). (b) Correlation coefficients of recruitment with monthly or seasonal minimum temperatures and monthly total precipitation (1961–2000). In both cases, the correlations were calculated for all months and seasons (spring, March–May; summer, June–August; autumn, September–November; winter, December–February). The black bars represent temperature and the grey bars represent precipitation. The significance level is indicated by the symbol over the bar (*indicates $P < 0.05$; #indicates $P < 0.1$).

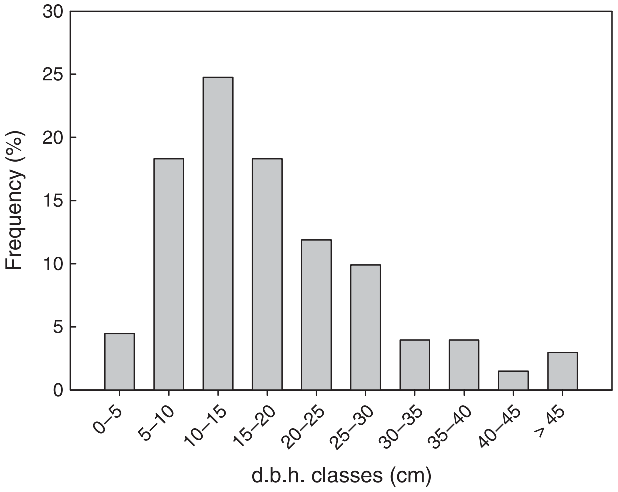

Figure 5 The d.b.h. (cm) distribution pattern of a *P. schreckiana* population at the treeline ecotone in the central Tianshan Mountains.

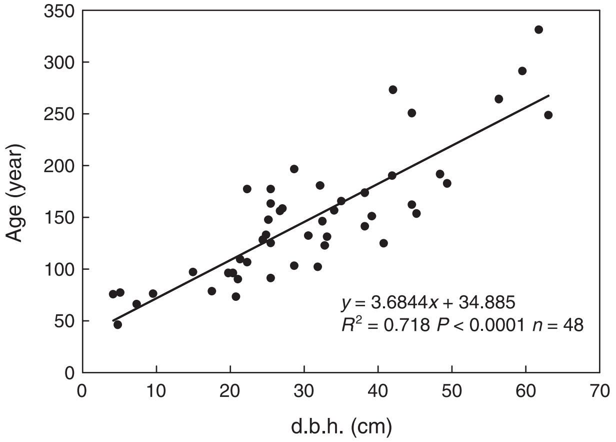

Figure 6 Relationship between tree age and d.b.h. of a *Picea schreckiana* population at the treeline ecotone in the central Tianshan Mountains.

indicated that Schrenk spruce in this stand might be a promising species for dendroclimatic studies (Table 2).

Schrenk spruce radial growth in the treeline zone was correlated positively with minimum temperatures in February and August. Warmer February temperatures benefit Schrenk spruce growth by promoting early snowmelt and increasing available soil water for growth in the early spring at these arid sites. Yuan & Li (1999) also showed that tree radial growth was correlated positively with higher winter temperatures in the Tianshan Mountains, and episodes of severe winter cold induced premature dieback of conifers at high elevations (Kullman, 1986; 1987a; Bradshaw, 1993). By using the relationship between tree-ring widths and climate variables, Yuan & Li (1999) reconstructed past winter temperatures successfully and concluded that there have been warmer conditions since the 1930s in the Tianshan Mountains.

Significant positive correlations were found between *P. schrenkiana* annual radial growth and precipitation of the current January and previous August. Above-average moisture during late summer and early autumn may promote storage of carbohydrates and bud formation, thus enhancing growth during the following year (Fritts, 1974; Oberhuber *et al.*, 1998; D'Arrigo *et al.*, 2001). Because some of the precipitation in January falls as snow, the positive correlations with January precipitation and February temperature may represent a relationship to snowpack and its subsequent effects on soil moisture (D'Arrigo *et al.*, 2001).

Seedling establishment and climate correlations

The age structure of a stand can provide a fairly accurate picture of temporal variations in the establishment rate (Kullman, 1991). The age structure of the Shrenk spruce forest growing at the treeline showed that trees could be dated back to the early 18th century. At least 35% of the *P. schrenkiana* population was older than 100 years, but only 16% was less than 50 years old (Fig. 3a). In the Tianshan Mountains, a good seed crop is produced every 4–5 years (Zhang & Tang, 1989), which suggests that seed production has not been a very important influence on the age structure distribution patterns across 5-year or 10-year age classes. Tree establishment at the treeline ecotone may be controlled mainly by local microenvironmental factors and episodic climatic events, leading to years of either low or high mortality (Szeicz & MacDonald, 1995).

This treeline ecotone is dominated mainly by arboreal *P. schrenkiana* with a *S. pseudosabina* understorey. The density and coverage of *P. schrenkiana* trees generally decreased, whereas the coverage of *S. pseudosabina* increased with increasing upslope elevation (Table 1). The great propensity of *S. pseudosabina* for its layering means that it is able to form dense mats 50–70 cm high. It was concluded that a high density of krummholz could create microenvironments favouring tree growth and establishment (Tranqullini, 1979; Hadley & Smith, 1987) because a dense krummholz-belt had a sheltering effect against the harsh treeline environmental conditions (strong wind and abrasion by ice, low temperature, e.g. Hadley & Smith, 1987; Weisberg & Baker, 1995). However, *P. schrenkiana* recruitment did not show an obvious correlation with tree density and the coverage of *S. pseudosabina* in the treeline of the Tianshan Mountains. The most striking feature of this treeline forest community is that there has been very little recruitment and establishment of new individuals of *P. schrenkiana* in the population over the last several decades.

A static age structure of living trees is the expression of change in the rate of tree recruitment and mortality over time (Harcombe, 1987). Successful recruitment and establishment is controlled mainly by favourable and sustained climatic conditions leading to a lower mortality (Szeicz & MacDonald, 1995; Camarero & Gutiérrez, 1999). In the upper treeline of the Tianshan Mountains, significant and positive correlations were found between recruitment (5-year classed) and total precipitation during June and spring (5-year average), but negative and significant correlations were found with rainfall in March and August (5-year average). High precipitation in March and August could cause higher soil moistures but colder soil temperatures in the early summer and late summer at the cold alpine treeline, which could be related to a shorter growing season and increased mortality due to colder conditions (lower daily minimum temperatures and more frosts, e.g. Camarero & Gutiérrez, 1999). The positive relationships between recruitment and precipitation in spring (March–May) and early summer (June) precipitation may reflect the high seedling mortality that occurs during spring–summer droughts (Camarero & Gutiérrez, 1999). It was found that *P. schrenkiana* recruitment was also favoured by high monthly minimum temperatures from May to late autumn (October), recruitment seemed to be favoured by high summer (June–August) temperatures with significant and positive correlations ($r = 0.646$, $P = 0.084$). In general, a wet spring (April and May) and warmer summer (June) over several successive years has favoured *P. schrenkiana* recruitment at this treeline zone during the last 40 years.

In the central Tianshan Mountains, the minimum winter temperature has increased by 0.055 °C per year since 1961, but the mean summer temperature has decreased at a rate of 0.002 °C per year. Cold summers may create unfavourable conditions for the establishment of *P. schrenkiana*. It has been shown that successful establishment is not related simply to temperature at the time of germination, but that the climate following germination is very important for establishment (Camarero & Gutiérrez, 1999). Camarero & Gutiérrez (1999) concluded that a 1-year-old seedling of *Pinus uncinata* often takes about 40 years to become a 2-m tall tree. Szeicz & MacDonald (1995) also showed that summer temperatures for up to 50 years following establishment are important in determining the recruitment success of white spruce (*P. glauca*), due most likely to its influence on seedling mortality rates (Black & Bliss, 1980; Kozlowski *et al*., 1991). Low summer temperatures over long time periods prevented reproduction and post-fire reforestation of *P. abies* at high elevation sites (Kullman, 1996), as the reproduction and establishment of *Picea* populations require warm summers over several successive years at the treeline (Kullman, 1983, 1987a). A similar long-term study in the Polar Ural treelines stated that the formation of an adult cohort of *Larix sibirica* at the treeline required favourable conditions for at least 50 years (Shiyatov, 1993).

Radial growth–tree recruitment correlations

The radial growth of *P. schrenkiana* increased with limited fluctuations in recent decades. The average ring-width index between 1951 and 2000 was 0.013 greater than during 1901–50 (Fig. 3b), but the recruitment and establishment of new individuals has been very rare during the last several decades (Fig. 3a). In some previous treeline studies, the climatic conditions that facilitate seedling establishment were similar to those conducive to the radial growth of trees (e.g. Kullman, 1987b; Szeicz & MacDonald, 1995; Camarero & Gutiérrez, 1999). Our results, however, showed that these two indices responded differently to temperature changes at the treeline (Fig. 4a,b).

At the upper treeline in the central Tianshan Mountains, the climatic conditions that facilitated *P. schrenkiana* seedling establishment were distinct and sometimes opposite to the conditions that facilitated the radial growth of krummholz trees (Fig. 4a,b). For example, low temperatures in June and July limited seedling establishment but favoured the tree's radial growth at most sites in the arid treeline of the central Tianshan Mountains. In addition, higher January precipitation availability favoured the tree's radial growth with more snowmelt in March but limited tree recruitment with colder early springs. Thus, years of high seedling frequency corresponded with higher spring precipitation and higher summer temperatures, whereas higher spring temperatures induced low moisture availability, limiting krummholz trees' radial growth in warm summers (Daniels & Veblen, 2004).

Treeline dynamics and climate change

As demonstrated in previous studies, climate can affect both tree recruitment and treeline advance rates. However, relationships between treeline shifts and climate change may be more complex. A treeline ascent implies several consecutive processes: production of viable seeds, dispersal, availability of adequate regeneration sites, germination, seedling survival and persistence until the individual reaches adulthood. Climate variability affects all these sequential stages, but the same climatic variable can enhance one of these processes while inhibiting another one (Earle, 1993; Camarero & Gutiérrez, 2004). Furthermore, mature trees are affected only slightly by climatic changes as compared to seedling and saplings (Kullman, 1993). The remains of mature trees therefore are much more likely to be preserved and may be used to investigate the importance of climate in determining mortality patterns. Long-term survival of marginal populations may be enhanced further as a result of local microclimatic modifications by tree islands or individual stems (Scott *et al.*, 1993).

At our site, the oldest trees established in the early eighteenth century, and many *P. schrenkiana* individuals (57%) established between 1890 and the 1940s, which probably form the current treeline zone. Fossil pollen analyses also indicated that *P. schrenkiana* at this marginal site survived throughout a long period of fluctuating climatic conditions, and the current timberline is about 250 m higher than in AD 550 (Yan *et al.*, 2003). However, the treeline has not shifted during the last several decades, even with rare recruitment of *P. schrenkiana*. The recent global warming is unlikely to cause an altitudinal ascent of the studied treelines when it is accompanied by a decrease in summer temperatures. It has been concluded that a directional increase in temperature, as predicted by current global climate scenarios, will not result consequentially in an upslope expansion of forests growing at altitudinal treeline (Camarero & Gutiérrez, 2004; Daniels & Veblen, 2004). Our results are very different from other studies on alpine treelines which have documented an altitudinal shift during the first half of the twentieth century followed by tree-density increases within the ecotone during the last decades (Rochefort *et al.*, 1994; Szeicz & MacDonald, 1995; Camarero & Gutiérrez, 2004). Accordingly, our results are similar to the very few studies that have shown that upward shifts in treelines have ceased since the 1950s, or earlier in certain regions, because climate stress and disturbance increasingly affect trees and ground cover (Kullman, 1996, 1998).

Some treeline individuals can persist for decades to centuries during harsh climatic periods and respond with an accelerated vertical growth in response to improved climatic conditions (Camarero & Gutiérrez, 2004). If the climatic threshold is surpassed due to an extreme climatic event (such as severe frost or intense warming), unexpected treeline shifts could result (Kullman, 1990; Camarero & Gutiérrez, 2004). Our results support the hypothesis that recruitment/survival patterns at the treeline are episodic and driven in part by long-term summer temperatures (Szeicz & MacDonald, 1995) and that the treeline would remain static until the climatic threshold is surpassed, which would result in sharp boundaries between the old and the new treelines (Camarero & Gutiérrez, 2004).

CONCLUSIONS

This study has documented the climatic response of radial growth and recruitment of *P. schrenkiana* growing at the treeline of the central Tianshan Mountains. In summary, both the climatic and dendroecological data document climatic warming in recent decades, but the response of radial growth and regeneration to temperature changes were very different in this arid and cold high treeline in the central Tianshan Mountains. The tree's radial growth was correlated positively with February and August temperatures, whereas the population age structure indicated that successful establishment was related to high minimum summer temperatures and spring precipitation over several successive years. As a result, both dendroclimatology and recruitment analysis were all valid and helpful to understand and reconstruct treeline dynamics correctly in the central Tianshan Mountains.

Our results are similar to findings by Camarero & Gutiérrez (1999, 2004), who showed that warmer summers over several successive years favoured reproduction and establishment in treeline populations, but higher temperatures are not the only climatic factor stimulating an upward shift in altitudinal treelines. We conclude that a directional increase in temperature will not necessarily result in an upslope shift of the *P. schrenkiana* forests growing at altitudinal treeline in the central Tianshan Mountains. The treeline would remain static until the climatic threshold is surpassed, resulting in conditions conducive to more successful establishment. While the correlations between age structure and climate change are not clear, its potential application for documenting global change should also be considered. Studies on the age structure of treelines, in combination with tree radial growth and climatic records, will be helpful in reconstructing historical climates as well as improving our understanding of plant–environment interactions and treeline dynamics. More detailed studies on the relationships between climatic change and forest regeneration rates are needed, which are especially important for understanding and predicting the ecological consequences of global warming on the dynamics of the uppermost distribution limits of forests located in remote sites.

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