

Climate constraints on growth and recruitment patterns of *Abies faxoniana* over altitudinal gradients in the Wanglang Natural Reserve, eastern Tibetan Plateau

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Abstract. The radial growth and recruitment patterns of trees in subalpine areas are subject to the influence of changing environmental conditions associated with changes in elevation. To investigate responses of fir radial growth and recruitment to climate factors at different elevations, tree-ring width chronologies and age structures of *Abies faxoniana* were developed from five sampling sites at ~2800–3300 m elevation on the north-western and south-eastern aspects in the Wanglang Natural Reserve on the eastern edge of Tibetan Plateau. Statistical characteristics of the chronologies indicated that expressed population signal and signal-to-noise ratio increased with increasing elevation in the north-western aspect; the reverse was observed on the south-eastern aspect. Correlation analysis between chronologies and climate variables showed that fir radial growth was negatively correlated with previous growing season mean temperatures and was positively correlated with January precipitation in all plots. The amount of precipitation in the growing season (June and July) greatly influenced radial growth in the two lower sites of both the aspects. The three plots on the north-western aspect were characterised by significant rates of tree recruitment in the past five decades. There were multi-decadal periods of heightened recruitment over the past three centuries in the two south-eastern plots. Widespread disturbances after 1920s were not observed in any plots and the infrequent small-scale disturbances that occurred were not the main factors influencing recent recruitment in any plots. Correlation analysis between recruitment residuals and climate variables showed that fir seedling recruitment in the north-western aspect plots was mainly controlled by spring–summer temperatures. But recruitment was greatly restricted by competition with dense bamboos and other tree species in the south-eastern aspect. Overall, previous August mean temperature and January precipitation were the dominant factors determining fir radial growth in all plots, and recruitment was sensitive to spring–summer temperatures in the plots with sparse bamboo cover.

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Introduction

Tree growth and recruitment are two key ecological processes of forest dynamics (North *et al.* 2004; Gutierrez *et al.* 2008), in which climate change and disturbances affect population structure, recruitment pattern and growth variation of tree species, especially over high latitude and altitude regions (Kullman 2002; Daniels and Veblen 2004; Dang *et al.* 2010; Liang *et al.* 2010; Lv and Zhang 2012). Mountain environments are an important component of the global biogeosphere (Peng *et al.* 2008), and mountainous ecosystems are considered to be much more sensitive and vulnerable to climate change, especially warming, than low plains (Messerli and Ives 1997). Other components of topography, particularly slope aspect, will interact with elevation to make the climate patterns and, therefore, tree growth and regeneration responses, much more complex (e.g. Daniels and Veblen 2004; Dang *et al.* 2009b; Elliott

and Kipfmüller 2011). Previous studies in many mountainous areas have reported that climate-growth relationships might vary along altitudinal gradients (Splechtina *et al.* 2000; Takahashi *et al.* 2003; Yu *et al.* 2006; Dang *et al.* 2007; Massaccesi *et al.* 2008; Peng *et al.* 2008; Brookhouse and Bi 2009) and the importance of limiting factors may vary in shaping forest regeneration with altitude (Duan *et al.* 2009). Tree recruitment in high-altitude areas, such as tree-line ecotones, is mainly controlled by climate (Szeicz and Macdonald 1995; Camarero and Gutiérrez 2004; Wang *et al.* 2006; Dang *et al.* 2009b). However, at lower altitudes tree regeneration may mainly be influenced by light availability, intraspecific competition (Duan *et al.* 2009), interspecific competition (Taylor *et al.* 2004; Dang *et al.* 2010) and disturbances (Lv and Zhang 2012) in addition to climate variables (Jump *et al.* 2007). In order to better understand the diversity of patterns of tree growth and recruitment in different

regions, additional studies along altitudinal gradients are required (Lv and Zhang 2012).

The Tibet Plateau (TP) is the highest plateau on earth with an average altitude over 4000 m above sea level. This unique physiographic and forest landscape is an ideal region to investigate forest dynamics along different altitudinal and topographical aspects. Previous studies using tree-ring data in the TP have focused on reconstructing historical climate (Liang *et al.* 2010), because tree-rings provide very good proxy records of past environments (Leal *et al.* 2008; Speer 2010). A growing number of studies of species- and site-dependent variability in tree growth and recruitment have also been carried out on the TP. Thus, on the southern TP, the recruitment of *Abies spectabilis* at the timberline is sensitive to summer temperature and is mainly controlled by disturbance in lower altitudes in the Mt Everest region (Lv and Zhang 2012). On the south-eastern TP, the growth of *A. georgei* var. *smithii* (Smith fir) is controlled by common climatic signals across different altitudinal gradients and different aspects (Liang *et al.* 2010). There has been minimal change in the Smith fir treeline position with recent warming (Liang *et al.* 2011) in the Sygera Mountains. However, little is known about variation in fir growth and recruitment history along topographic and altitudinal gradients in subalpine areas on the eastern edge of TP.

The Wanglang Natural Reserve, located on the eastern edge of TP, is a key habitat corridor for giant panda, an endangered species with a very strict food requirement, eating *Fargesia denudata*. This bamboo competes with coniferous forests in the region and *Abies faxoniana* is one of key species present in these subalpine coniferous forests. *Abies faxoniana* is distributed over its entire altitudinal range in the Wanglang Natural Reserve, thereby allowing for an exploration of how fir growth and recruitment varies with elevation. *Abies faxoniana* has been considered an ideal tree species to explore the influence of global change, including responses to enhanced UV-B radiation (Liu *et al.* 2011) and nitrogen supply (Yao and Liu 2009; Liu *et al.* 2011), elevated atmospheric CO₂ concentration and elevated temperature (Hou *et al.* 2010, 2011; Wang *et al.* 2012). However, our knowledge of the effects of long-term climate variability on *A. faxoniana* in these subalpine forests is limited.

In this study, we assessed patterns of *A. faxoniana* radial growth and establishment relative to temperature and precipitation on north-western and south-eastern aspects within the Wanglang Natural Reserve. Due to the influence of the south-east monsoon (Pu *et al.* 2008; Yao *et al.* 2010), the conditions of temperature, precipitation and light are slightly different between south-eastern aspect and north-western aspect in Wanglang Natural Reserve. We used tree-ring analysis to examine radial growth patterns and regeneration dynamics of the dominant tree species, with the following specific objectives: (1) to examine spatial and temporal variability in radial growth and recruitment of *A. faxoniana* forest over altitudinal gradients on two different aspects in the Wanglang Natural Reserve; (2) to identify the main climate factors to influence fir radial growth and recruitment and how this may change with altitude; and (3) to identify whether disturbances influence the observed patterns in recent recruitment.

Materials and methods

Study area

This study was performed in the Wanglang Natural Reserve (32°49'–33°02'N, 103°55'–104°10'E) in the Min Mountains, on the eastern edge of TP in western Sichuan Province, where *A. faxoniana* is the dominant tree species (Fig. 1). This area was selected because: (1) the area is covered with old forest that has been little affected by anthropogenic disturbance; (2) the semi-humid, cold climate of this subalpine area suggests that tree growth and establishment may be sensitive to climate variation; and (3) the steep and deeply dissected terrain includes topographical conditions that allow an examination of the influence of aspect on fir growth and recruitment.

The Wanglang Natural Reserve is located in the Himalayas-Hengduan Mountains, a global biodiversity hotspot. Elevations in the reserve range from 2300 to 4980 m. Our sites were selected from an elevation of ~2800 m to the upper treeline (an average of ~3300 m) because conifer forests below 2700 m had been clear-felled since 1950s until 1964 when the reserve was established (Taylor *et al.* 2006). The study area is within a Danba-Songpan semi-humid climate, characterised by dry, cold winters and wet, cool summers (Fig. 2). The average temperature is 12.7°C in July and –6.1°C in January, with a recorded maximum temperature of 26.2°C and minimum temperature of –17.8°C. The mean annual precipitation is ~1100 mm. The annual rainy season may last more than 195 days and is concentrated from May to September (Fig. 2). Annual average temperature has increased but annual precipitation has decreased since the 1950s (Fig. 2). The soils in the reserve are classified as mountain brown soils, mountain dark brown soils and alpine meadow soils. In this area, the main mountain ridges all run north-east to south-west. The south-eastern aspect is wetter and warmer than the north-western aspect, and receives more solar radiation.

Field survey

Field work was carried out in the summer of 2010. Five sites, three on the north-western (NW) aspect (NW-2903, NW-3141 and NW-3297) and two on the south-eastern (SE) aspect (SE-2866 and SE-3225), were selected (Table 1). The plots NW-3297 and SE-3225 were located in the upper treeline of *A. faxoniana* on NW aspect and SE aspect, respectively. At each site, a rectangular plot (100 × 20 m) was established with the longer side running along the elevation contour to diminish climate difference within each sampling sites.

Within each plot, all living trees were recorded and the DBH (diameter at breast height, 1.3 m above ground level) of each adult living tree (>2 m in height) was measured and one or two cores per adult fir tree were extracted in the direction parallel to the slope contour using increment bores. The number of branch whorls and bud scars on the main stem of fir seedlings (<0.5 m in height) and saplings (0.5–2 m in height) were counted to determine their approximate age (Daniels and Veblen 2004). In total, 581 increment cores from 314 adult trees were sampled and 899 saplings and seedlings were measured in all the plots. In addition, 68 seedlings and saplings with a normal growth form were randomly chosen and uprooted to create an age-height regression to estimate the time required for young firs to reach

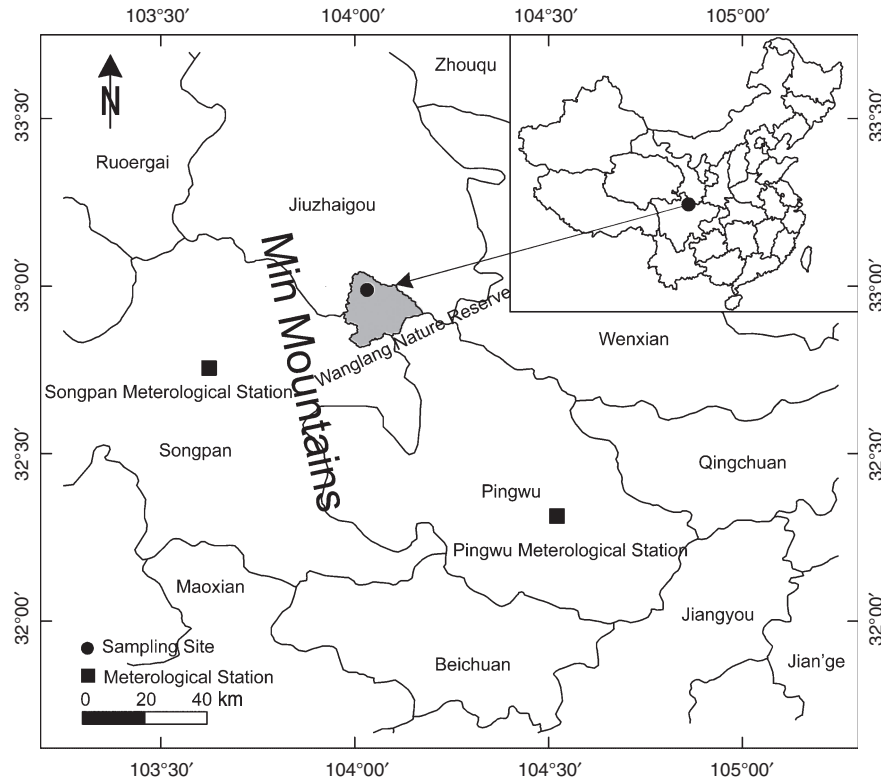


Fig. 1. Study area, sampling site, meteorological stations, and location of study area in China.

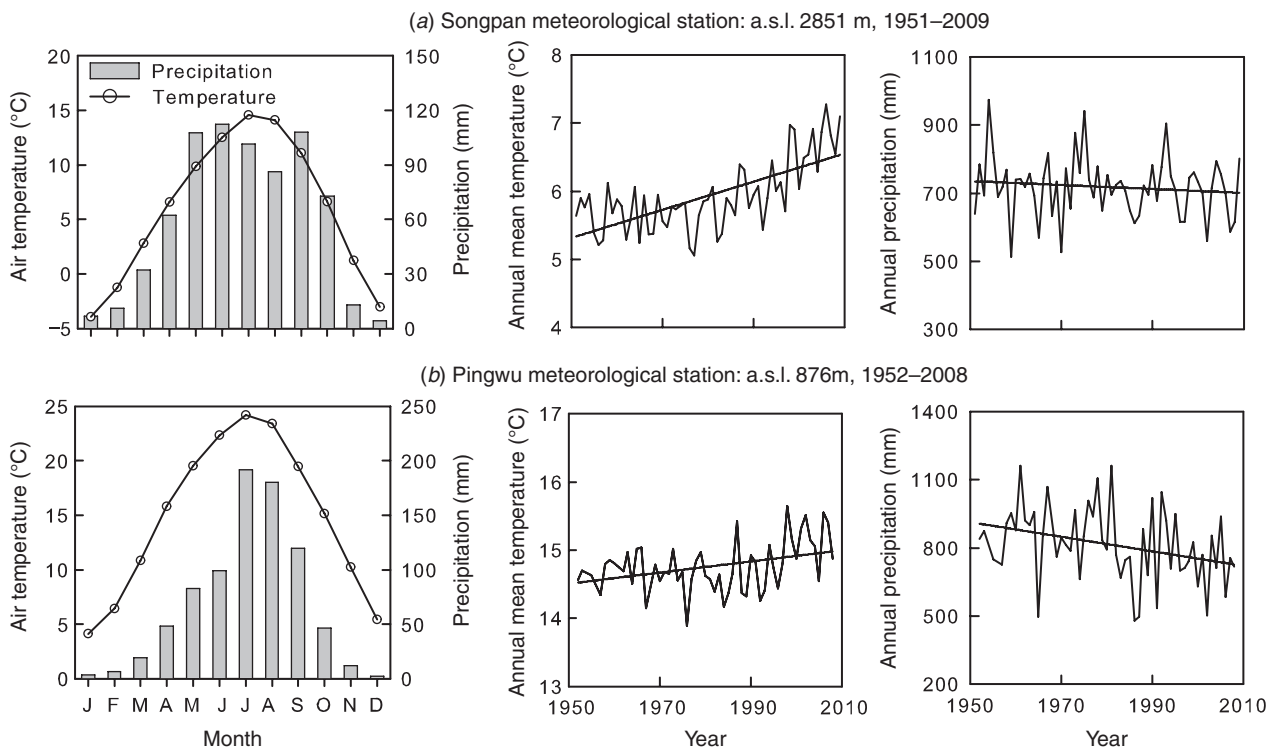


Fig. 2. Climate of the two meteorological stations near the sampling sites in the Min Mountains on the eastern edge of the Tibet Plateau.

Table 1. Characteristics of the sampling sites in the Wanglang Natural Reserve
The forest stand codes indicate the slope aspect (NW and SE) followed by the stand elevation

Site code	NW-2903	NW-3141	NW-3297	SE-2866	SE-3225
Latitude	33°00.4'N	32°59.6'N	32°59.5'N	32°55.6'N	32°54.2'N
Longitude	104°01.6'E	104°01.9'E	104°01.7'E	104°03.7'E	104°02.9'E
Elevation (m)	2903	3141	3297	2866	3225
Slope %	10	15	12	15	20
No. of adult fir trees	81	65	53	49	66
No. of fir seedlings and saplings	90	165	599	29	16
No. of other trees	35	128	220	54	75
Bamboo cover (%)	22.21	6.75	19.53	31.55	42.25

the coring height (~1.3 m). The number of branches and scars of the 68 seedlings/saplings were also recorded to assess the underestimated errors of the age data (see below).

Chronology development and age estimation

Air-dried increment cores were mounted on stands and sanded with progressively finer grades of sandpaper to produce a flat and polished surface on which annual rings could be easily distinguished. Ring widths were measured using a LINTAB II measuring system, with 0.01-mm precision. All measured tree-ring sequences were quality-checked with the computer program COFECHA (Holmes 1983). All cores with measurement mistakes were rechecked and corrected by the software packages TSAP-Win (Rinn 2003). We excluded any cores that were physically broken in the coring process, shorter than the available climate data (i.e. 1951–2009: 59 years), or unable to be crossdated. This led to relatively high rejection rates (primarily due to the exclusion of young trees). Our final tree-ring chronologies were ultimately based on a total of 321 cores from 210 trees. These cores were also used for fir release and age structure analyses.

Tree-ring chronologies were constructed for each site using ARSTAN (Cook 1985). In order to remove or minimise long-term and low-frequency trends due to stand dynamics, most of series were detrended with negative exponential curves or linear regression (Szeicz and MacDonald 1994). If both curve types failed to fit the time series, an 80-year cubic smoothing spline with a 50% frequency-response cut-off was applied. A data-adaptive power transformation was used to stabilise the variance and mitigate non-normality in the series before detrending (Liang *et al.* 2010). Then tree-ring indices as residuals were calculated between the power-transformed raw measurements and fitted values. Detrended series were averaged using the bi-weight robust mean to generate the residual chronologies.

For adult fir trees, tree ages were determined by adding the estimated number of years for young firs to reach breast height onto the ring counts of cores. When the pith of core was missing, the number of rings to the pith was estimated using a geometrical method. For incomplete cores that did not show curvature in the innermost rings, age was determined by the age-DBH. regression model. From the correlation between age (y , year) and height (x , cm) of the fir seedlings ($y = 0.180x + 4.615$, $R^2 = 0.728$, $P < 0.001$, $n = 68$); fir trees at this site typically take 29 years to reach 1.3 m. For seedlings and saplings, ages were determined by the number of whorls and scars on their main stem. The age distribution was presented at 10-year intervals to eliminate

possible errors in the age determination process (Dang *et al.* 2010).

Growth release analysis

The percentage growth change filter (Nowacki and Abrams 1997) was applied to the fir tree-ring series to identify past disturbances that affected the canopy in each sampling site. 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). Growth release was identified using the formula as follows:

$$\%GC_r = [(M_2 - M_1)/M_1] \times 100 \quad (1)$$

where $\%GC_r$ is the percentage growth release between preceding and subsequent 10-year means, and M_1 and M_2 is the preceding and subsequent 10-year ring-width mean width, respectively. We defined a growth release event as a 50% increase in average radial growth of the current year relative to the previous year, lasting for at least 10 years afterwards (Lv and Zhang 2012). Stand-wide disturbance events were specifically denoted at peaks comprised of 25% of the sample trees (Nowacki and Abrams 1997). This criterion, coupled with tree canopy recruitment dates, was used to distinguish disturbance events from responses attributed to climatic factors (Abrams and Orwig 1996).

Climate data

Climate data (1951–2009) from the nearest meteorological station, Songpan base station (32°39'N, 103°34'E, 2850 m above sea level, ~55 km south-west of the sampling sites), were used in the study. In order to emphasise spatial variability across sampled sites, the Mountain Climate Simulator (MTCLIM) (version 4.3; developed by School of Forestry, University of Montana, Bozeman) was employed to derive climate variables for each sampling site. The program MTCLIM uses daily observations from one location to estimate climatic factors for another, especially in mountainous terrains (Dang *et al.* 2007). The simulated results showed that the mean annual temperature of plot SE-2866 is 2.4°C higher than that of plot NW-3297.

Dendroclimatic and climate-recruitment analysis

Radial climate-growth relationships were examined between residual chronologies and the climatic variables for the period

1951–2009 by standard correlation function analysis (Fritts 1976). The analyses were performed with the program Dendroclim2002 (Biondi and Waikul 2004), using the monthly mean temperature and monthly precipitation derived from the program MTCLIM. Because radial growth may often be affected by the climate of the previous growing season (Fritts 1976), climatic variables from the July of the previous growth year to the September of the current growth year were used to analyse the growth-climate relationships.

The influence of climate on seedling recruitment was tested by Pearson's correlation coefficients between recruitment residuals with the derived climatic variables during 1951–2009 (Szeicz and Macdonald 1995; Daniels and Veblen 2004). Because counting the branch whorls and bud scars may underestimate the true fir seedling age (Liang *et al.* 2011), we compared the differences between the discs' ages of the uprooted 68 seedlings and saplings and their number of whorls and scars to improve the resolution of the age date. We found that only 20% of the samples were accurate, 15% were being underestimated by 1 year, 20% were being underestimated 1 year and 45% were being underestimated by 3 or more years. Consequently the age frequency of fir seedlings and saplings was smoothed by the formula as follows (Daniels and Veblen 2004):

$$x_t = 0.20(f_t) + 0.15(f_{t-1}) + 0.2(f_{t-2}) + 0.45(f_{t-3}) \quad (2)$$

where x is the smoothed age frequency, f is the original age frequency, and t is the year of seedling recruitment. In order to account for mortality of young firs, the age frequencies of fir seedlings and saplings were detrended by fitting two theoretical distributions, namely the exponential and power functions (Hett and Loucks 1976). The best-fit distribution (statistical significance at the $\alpha=0.05$, high values of adjusted r^2 and low standard error) was selected for further analysis (Szeicz and

Macdonald 1995; Daniels and Veblen 2004; Lv and Zhang 2012). The differences between theoretical age frequencies and observed age frequencies provided time series of recruitment residuals (Szeicz and Macdonald 1995). Then the 'recruitment residuals' were used to analyse the climate-recruitment relationships. The climatic variables included monthly mean temperature and monthly precipitation from January to December (Jump *et al.* 2007).

Results

Plot structure

Approximately 95% of the fir seedlings were found in the three plots of NW aspect, especially in the plot NW-3297, and few seedlings and saplings were found in the two SE plots (Table 1). The number of fir seedlings and saplings showed an increasing trend along the altitudinal gradients in the NW facing plots. Most of the other trees (67.8%) were mainly distributed in the two higher plots of NW aspect. The bamboo cover in each SE plot was much higher than that in each NW plot.

The fir population (5-cm DBH classes) showed a typical 'L'-shape size distribution pattern in the three NW plots (Fig. 3). The fir individuals in the <5-cm DBH classes accounted for 47.1, 49.7, 67.8% of the total tree species in plots NW-2903, NW-3141 and NW-3297, respectively. In the two plots SE-2866 and SE-3225, other tree species occupied a larger proportion in the >5-cm DBH classes (Fig. 3).

Radial growth patterns and disturbance history

Residual chronologies for *A. faxoniiana* and their characteristics are presented in Fig. 4 and Table 2. The chronologies for all the sites in both aspects demonstrated similar patterns, with characteristic narrow rings in the same pointer years, such as 1935–37, 1967, 1976, and 1982 (Fig. 4). Mean ring-widths in both aspects displayed consistent reductions with increasing

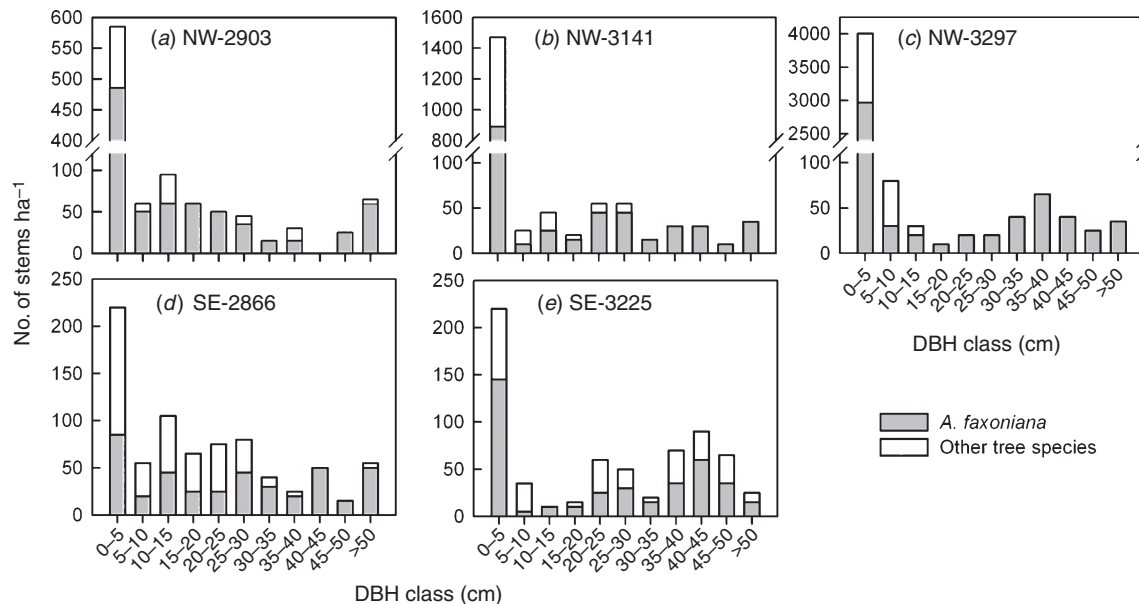


Fig. 3. The densities of main trees (number of stems ha^{-1}) in 5-cm diameter at breast height (DBH) classes in the five sampling plots in the Wanglang Natural Reserve. Data for *A. faxoniiana* only (grey bars) and for all other tree species pooled (white bars) are shown.

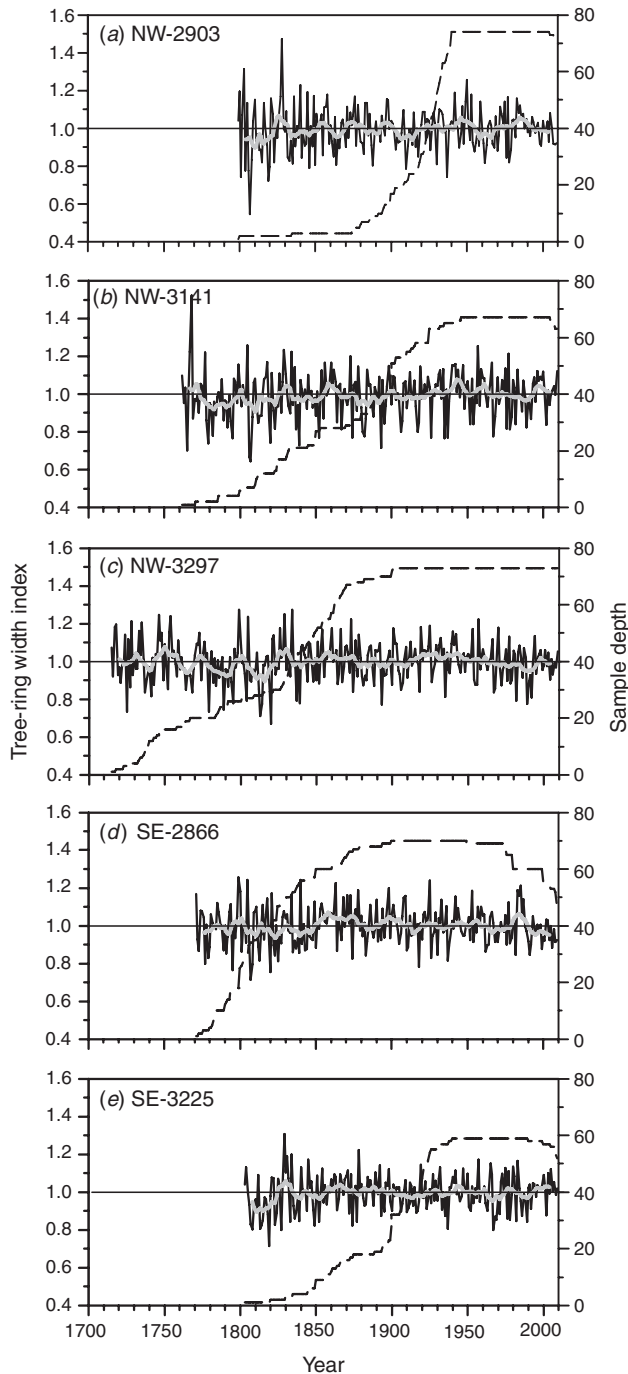


Fig. 4. Tree-ring width residual chronologies of *A. faxoniana* with sample depth (number of cores). Solid back thin and grey thick lines represent the tree-ring width indices and their 10-year moving average, respectively; the dashed line shows the number of cores.

elevation (Table 2). The mean sensitivity (MS) for each chronology was not high, ranging from 0.115 to 0.144 (Table 2). The NW sites generally had a larger MS and standard deviation (s.d.) than the SE sites (Table 2). The largest mean series inter-correlations occurred in the mid-elevation plot of NW aspect (NW-3141). The expressed

population signal (EPS) and signal-to-noise ratio (SNR) in the NW upper site (NW-3297) were much larger than those in the SE upper site (SE-3225). In general, no obviously increasing growth trends were found for any of the stands since the 1950s except several small fluctuations (Fig. 4).

The radial growth release analysis revealed local disturbances at small scales (Fig. 5). There was only one distinct peak in growth releases in our tree-ring record. This occurred in NW3297 from 1820 to 1830 and followed the period of lowest growth in the tree-ring chronology during 1810–20, which included the two narrowest rings in 1813 and 1820 (Fig. 4). No standwide disturbances were found in any of the five plots after 1920s (Fig. 5).

Age structure and recruitment patterns

The establishment distribution of fir trees over time for all the plots is shown in Fig. 6. The oldest individuals were >300 years old (established before 1710) in both NW and SE aspects. In plots having a NW aspect, from the lower elevation to the upper limit, most of the fir trees were younger than 50 years in each plot, 46, 69 and 90% in NW-2903, NW-3141 and NW-3297, respectively. In the SE aspect, 43% of fir trees were between 230 and 270 years old (recruited between 1760s and 1820s) in the lower plot (SE-2866), and 65% of fir trees were between 150 and 220 years old (between 1790s and 1870s) in the upper plot (SE-3225).

The fir populations in the three NW plots showed that the young firs were successfully recruited during the last 60 years (Fig. 6). Trends of increasing recruitment during the past 30 years were also observed in the SE plots (Fig. 6), although the frequency of seedlings and saplings was low in these two plots (29 for SE-2866 and 16 for SE-3225) (Table 1).

Correlations with climate

Analysis of climate-growth relationships showed that all five chronologies were negatively correlated with the monthly mean temperature in the previous growing season (Fig. 7). This was an especially strong correlation for the previous August mean temperature across all chronologies (Fig. 7). Almost no consistent correlations were found between tree growth and monthly mean temperatures in the current year, although fir radial growth at the high-elevation NW stand (NW-3297) was significantly and positively correlated with the mean temperature in April. Mean temperature in the current September was significantly and negatively correlated with tree growth at the low-elevation SE stand (SE-2866). Tree growth across all stands showed a positive correlation with total precipitation in January, significantly so at NW-3141, NW-3297 and SE-2866 (Fig. 7). In the NW plots, site chronology showed a significant positive correlation with precipitation in the previous September at the low-elevation stand (NW-2903), and precipitation in current September demonstrated significant negative correlation with the site chronology in the high-elevation stand (NW-3297). In plots having a SE aspect, the low-elevation forest chronology (SE-2866) was significantly and positively correlated with the current July precipitation but significantly and negatively correlated with precipitation in the previous October (Fig. 7). No significant correlations were found between radial growth and precipitation in the high-elevation forest (SE-3225).

Table 2. Dendrochronological statistics for the *A. faxoniana* residual chronologies in the Wanglang Natural Reserve

Site code	NW-2903	NW-3141	NW-3297	SE-2866	SE-3225
No. of trees/cores	74/56	67/45	73/38	48/30	59/41
Record period	1799–2009	1762–2009	1715–2009	1771–2009	1803–2009
Median age of trees	85	125	178	190	110
Mean ring-width (mm)	1.666	1.159	0.913	1.117	1.059
Expressed population signal >0.85 since	1905	1815	1750	1810	1870
Mean sensitivity	0.144	0.140	0.132	0.124	0.115
s.d.	0.119	0.121	0.108	0.104	0.096
Autocorrelation order 1	–0.167	–0.045	–0.155	–0.155	–0.048
Common interval analysis	1930–2009	–	–	–	–
Mean correlations					
R_1 (among all radii)	0.304	0.378	0.357	0.323	0.299
R_2 (between trees)	0.301	0.374	0.354	0.319	0.296
R_3 (within trees)	0.581	0.624	0.570	0.589	0.546
Express population signal	0.955	0.973	0.976	0.958	0.954
Signal-to-noise ratio	21.405	35.805	40.592	22.934	20.917
PC1% (variance 1st eigenvector)	32.5	39.3	37.1	34.3	32.1

Correlation analysis of climatic data with fir recruitment-residuals showed similar results for the three-altitudinal stands having a NW aspect (Fig. 8). High temperatures in the spring and summer seasons were the main factors enhancing recruitment of fir seedlings. Recruitment at the lowest NW plot (NW-2903) was significantly and positively correlated with mean temperature in September (Fig. 8). At the mid-altitudinal forest (NW-3141), significant positive correlations were found between June mean temperature and recruitment. In the upper stand (NW-3297), fir recruitment was significantly and positively correlated with mean temperatures in April, July and September. Precipitations showed no significant correlation with the recruitment in all of the three stands (Fig. 8).

Discussion

Radial growth and climate

Differences in radial growth rates of *A. faxoniana* were found at different elevations. That radial growth rates declined with increasing elevation in this study was consistent with previous studies of growth over altitudinal gradients (Dang et al. 2007; Massaccesi et al. 2008; Liang et al. 2010). The lower temperatures at high altitudes limit physiological processes (especially C gain and photosynthetic processes) responsible for tissue formation (Körner 2003), while strong wind exposure, shallow soil and low nutrient availability (Liang et al. 2010) also contribute to decreased radial growth rates observed at high elevations. The low MS among all the five sites (Table 2) indicated that tree-ring variability was relatively low. This result was similar to that of other temperature-sensitive species on the TP (Liang et al. 2006, 2010) and in the Tatra Mountains, Poland (Savva et al. 2006). Trees from temperature-limited habitats often show lower variability in growth than trees from moisture-limited sites (Liang et al. 2006).

Generally, the most useful parameters for evaluating the quality of a chronology were SNR, EPS and PC1 of the trees contained in the chronology (Peng et al. 2008). The values of SNR, EPS and PC1 for the chronologies in NW-3141 and

NW-3297 were much larger than those in the other three plots. This might indicate that tree growth was more strongly regulated by climate at the mid- and high-elevation plots than in the lower plot, in the NW aspect.

The radial growth patterns observed in the present study and their responses to temperature in the previous growing season and precipitation in January were similar in both the NW and SE aspects. Average temperatures of the previous summer, especially in previous August, had significant negative effects on *A. faxoniana* radial growth of the current year in both aspects (Fig. 7). Negative correlations between tree growth and previous growing season temperatures have been reported for other species in the south-eastern and southern TP (Liang and Wang et al. 2010; Lv and Zhang 2012) as well as other areas (Yu et al. 2006; Brookhouse and Bi 2009; Fang et al. 2010; Lo et al. 2010). It is possible that high temperatures in summer will intensify evapotranspiration and thus reduce available moisture content and consequently reduce radial growth (Lara et al. 2001; Savva et al. 2006; Fang et al. 2010). High temperatures in previous August may also lead to an increased rate of respiration and thus reduce or deplete food reserves for growth of the following year (Kozłowski et al. 1991; Liang et al. 2011). January precipitation showed a positive influence on radial growth in all the five sites (Fig. 7). Similar relationships between growth and winter precipitation have been found in other areas (D'Arrigo et al. 2001; Wang et al. 2006; Fan et al. 2008). The winter snow (the common form of winter precipitation) could be reservoir for next growing season's water supply (Lo et al. 2010).

The growth responses of *A. faxoniana* to climate varied across the observed altitudinal range. For the NW aspect plots, only at the high-elevation plot (NW-3297), did high April temperatures facilitate radial growth (Fig. 7). This result is consistent with previous studies demonstrating that temperatures in early spring limited ring-width increment at high elevations in other mountainous areas (Yu et al. 2006; Dang et al. 2009b; Fang et al. 2010). Warmer temperatures in spring lengthen the growing season (Case and Peterson 2005) and can result in early initiation of cambial activity and increased supply of photosynthates

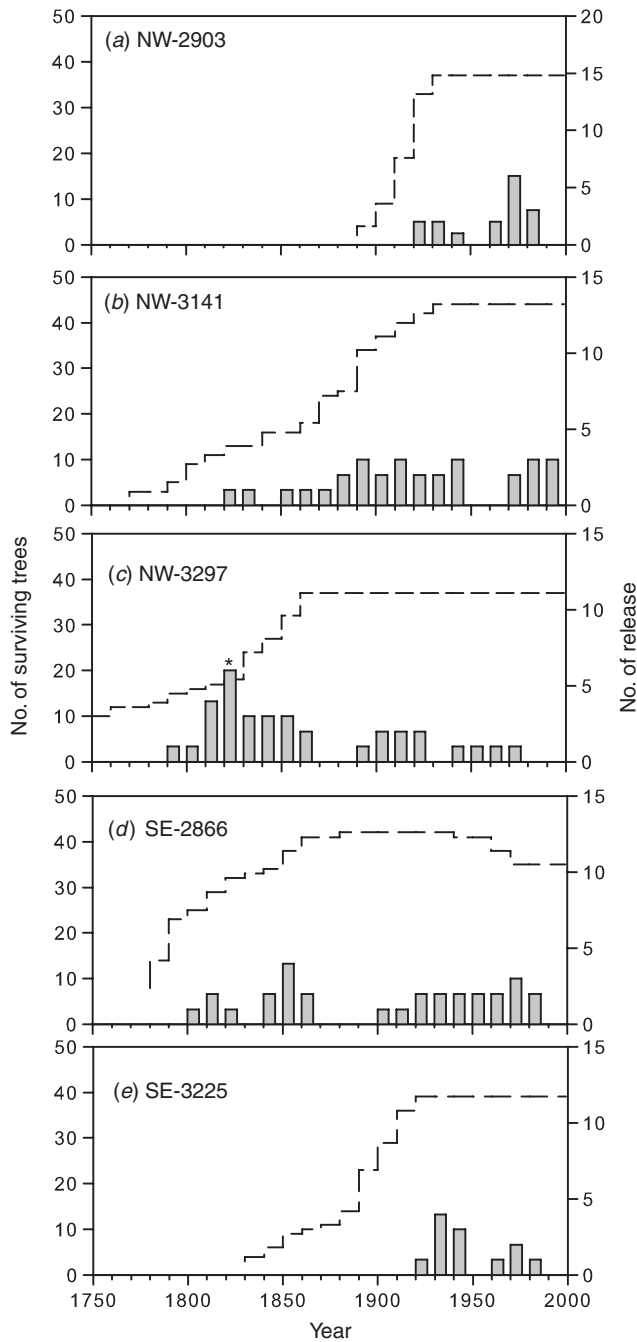


Fig. 5. Growth release analysis for the five sampling plots of fir forest in the Wanglang Natural Reserve. The number of trees showing release in corresponding 10-year intervals is indicated by bars and the number of surviving trees is indicated by dash lines. Asterisks indicate growth release peaks.

(Splechtna *et al.* 2000). In contrast, at the low-elevation site in the SE aspect (NW-2903), precipitation in the previous September positively influenced the next year's radial growth (Fig. 7). High precipitation in the end of the previous growing season may enhance photosynthetic rates and the production of sugars and result in more stored food reserves in branches and needles for the following growth (Takahashi *et al.* 2003). For the SE plots radial

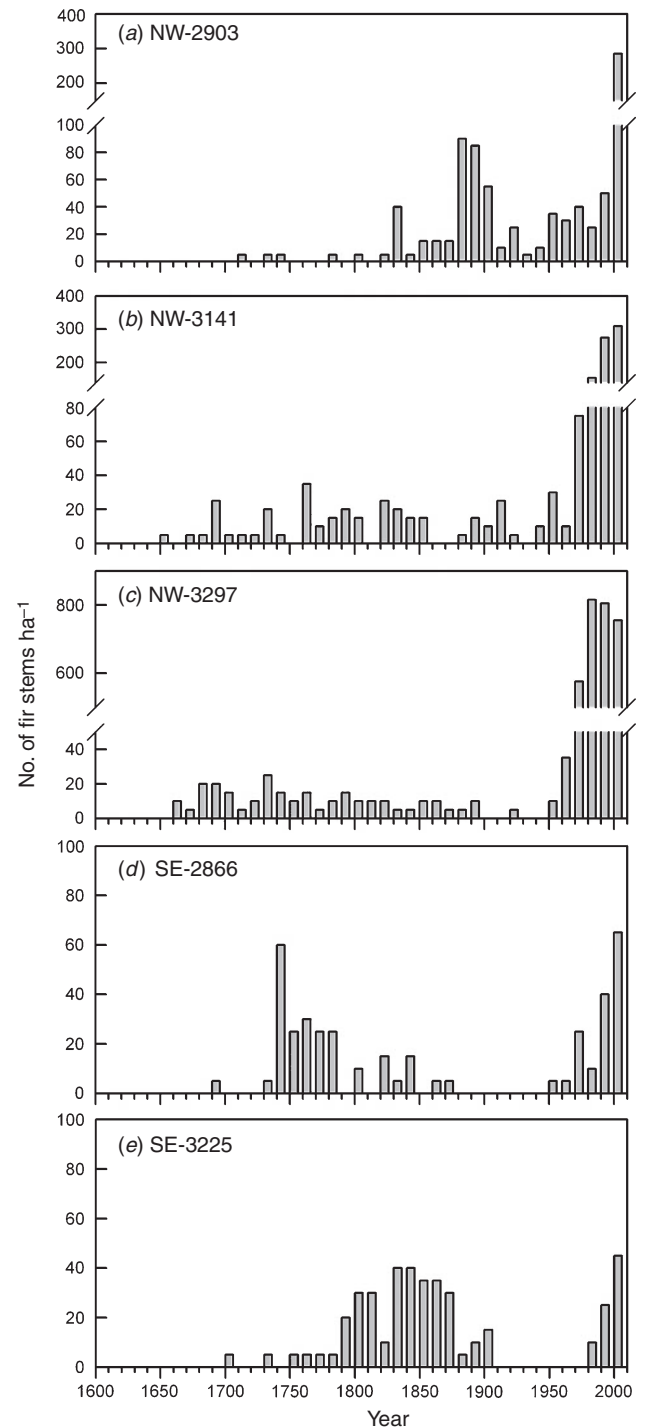


Fig. 6. The densities of *A. faxoniana* (number of fir stems ha^{-1}) in the five sampling plots in the Wanglang Natural Reserve. Numbers of fir recruitments are aligned into 10-year intervals.

growth at the low-elevation site (SE-2866) was significantly limited by high precipitation in the previous October (Fig. 7). The negative association with the previous October precipitation might be a response to mechanical damage from freezing rain or snows, leading to a decreased rate of radial growth in the

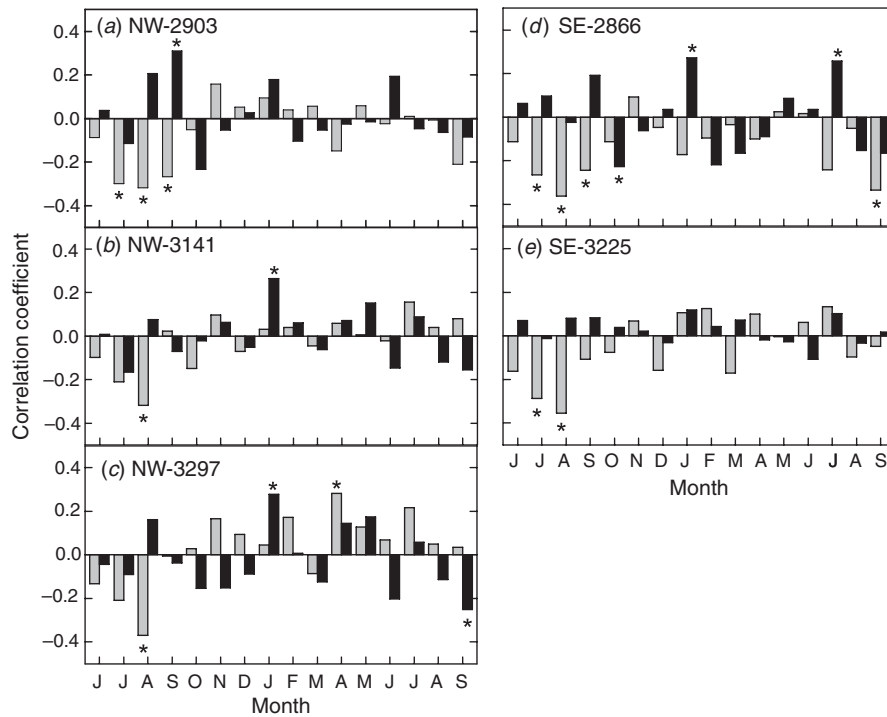


Fig. 7. Correlation coefficients between each tree-ring chronology of *A. faxoniana* with climatic variables from June of the previous year to September of the current year. The grey bars and black bars represent monthly mean temperature and monthly precipitation, respectively. * $P < 0.05$.

following year (Gedalof and Smith 2001). High precipitation in July of the current growing season had positive effects on tree growth at the low-elevation site (SE-2866). This positive correlation in the low-elevation zone has been also found in other mountains (Fang *et al.* 2010; Lo *et al.* 2010), suggesting that water stress during the growing season could be a limiting factor for radial growth during dry years (Case and Peterson 2005).

Overall, tree growth was strongly influenced by temperatures in both the NW and SE aspects, whereas precipitation in growing season played a more important role in radial growth at the two low-elevation sites. Similar results have been reported in the north-eastern TP (Peng *et al.* 2008) and other areas (e.g. Wang *et al.* 2005; Fang *et al.* 2010). This might be explained by the assumption that soil moisture increased with ascending elevation and thus precipitation in growing season was less important factor in controlling tree growth at the high-elevation sites than it did at the low-elevation sites (Wang *et al.* 2005; Peng *et al.* 2008). Furthermore, precipitation generally increased with the increase of elevation in this area because warm moist air flows will be easier to condense into rain under cold temperatures in higher elevations (Li 2006).

Recruitment and disturbance

The size and age distribution of forest stands can be used to interpret tree population dynamics in relation to past disturbance patterns (Cullen *et al.* 2001; Brown and Wu 2005). Both the size and age-structures of the NW stands indicated that environmental factors had little effect on the age structures in these stands (Duan *et al.* 2009). The irregular fir size and age structures in both SE

plots showed at least one recruitment peak occurred before 1900. Both size and age structures suggest that disturbances were not important factors determining recruitment rates in the NW plots (Lv and Zhang 2012).

No stand-wide disturbances (Fig. 5) but large numbers of seedlings and saplings (Fig. 6, Table 1) were detected in all three NW plots after 1950s, especially in the high-elevation site (NW-3297). Several studies have shown that conifer regeneration is dependent on large-scale disturbances (Dang *et al.* 2009a; Stueve *et al.* 2009; Lv and Zhang 2012), which produce large canopy openings and provide enough light and space for recruitment (Yamamoto 2000; Sapkota and Oden 2009). However, in southern interior British Columbia, the subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] establishment is largely unrelated to disturbance (Antos and Parish 2002). In our study, the recent fir recruitment observed in the NW plots might be more influenced by changes in climate, especially temperature, rather than the infrequently-observed small-scale disturbances. Although one peak of growth release occurred during 1820–30 in plot NW-3297, no obvious recruitment was found in the subsequent 180 years. The low sample replication showing release may not reflect the impact of disturbance well (Lv and Zhang 2012). This peak of growth release might be a result of the pronounced cold period ~1815–1822 in eastern Tibet (Bräuning 1994; Wu and Shao 1995; Cook *et al.* 2003). This unusual cold event might be caused by the Tambora eruption (Cook *et al.* 2003). Although a low rate of sample replication may have masked a recruitment response, we suggest that competition with bamboo and other species may have limited recruitment (see below).

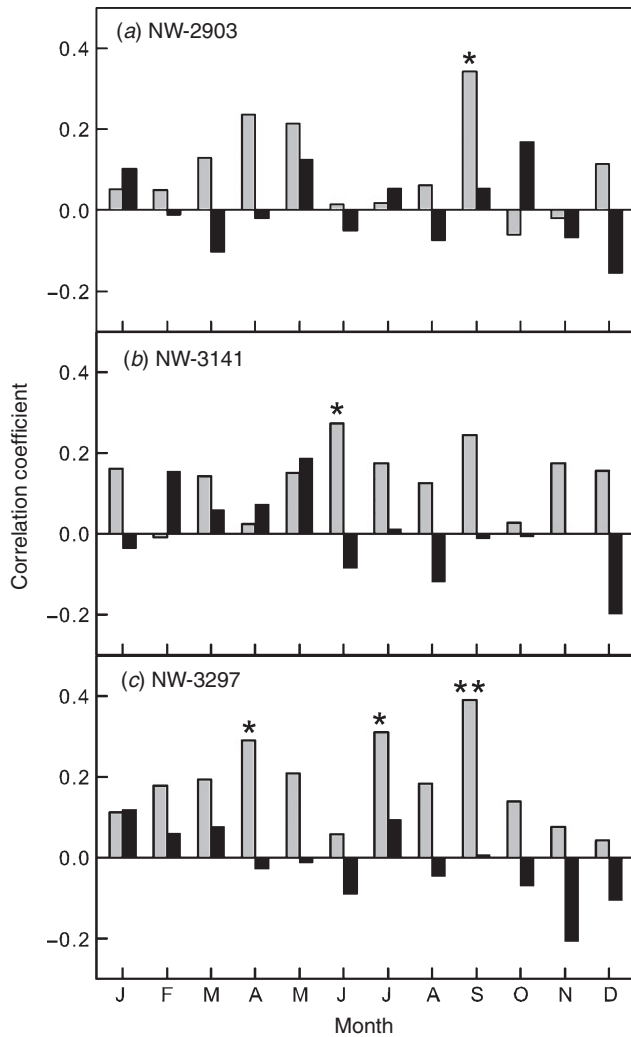


Fig. 8. Correlation coefficients between fir recruitment in the three sampling plots of north-western aspect with climatic variables from January to December. The grey bars and black bars represent monthly mean temperature and monthly precipitation, respectively. ** $P < 0.01$ and * $P < 0.05$.

Recent recruitment and climate

The correlations between recent recruitment and climate variables in the three NW plots showed that spring and summer temperatures were the main limiting factors to recruitment between 1951 and 2009. Furthermore, recruitment in the high-elevation site (NW-3297) was more sensitive to climate change than that in the two lower sites (NW-3141 and NW-2903) (Fig. 8). Positive relationships between spring–summer temperatures and tree recruitment have been reported widely for the upper treeline (Szeicz and Macdonald 1995; Camarero and Gutiérrez 1999, 2004; Dang *et al.* 2009b). High temperatures in spring can speed up snowmelt (Camarero and Gutiérrez 1999) and stimulate tree establishment from seed rain or the seed bank (Dang *et al.* 2009b). High summer temperatures have been shown to increase recruitment in the southern TP (Lv and Zhang 2012) and the south-eastern TP (Liang *et al.* 2011). Higher summer

temperatures are likely to increase total C gain during the summer and therefore increase non-structural C storage. This may increase survival rates of fir seedlings during the harsh winter climate. High temperatures during late summer (September) are likely to increase the length of the growing season and may reduce low temperature induced mortality (Camarero and Gutiérrez 1999). The influences of summer temperatures on seedling recruitment and tree radial growth were inconsistent (Figs 7, 8). The potential reason might be that higher summer temperatures effects on seedlings and mature trees could be different. For example, high summer temperatures would cause excessive transpiration and respiration for the mature fir trees, while seedlings might make better use of nutrient and water reserved in litters and moss on forest floor under high summer temperatures. Further and intensive studies may make these mechanisms clear. More significant correlations between recruitment and temperatures existing in the high-elevation site (NW-3297) were consistent with the hypothesis that tree recruitment is mainly controlled by climate (Camarero and Gutiérrez 2004; Wang *et al.* 2006; Lv and Zhang 2012). No significant correlations between precipitation and recruitment were observed in the present study and therefore precipitation does not appear to be a major factor influencing regeneration in this area.

Other factors affecting recent fir recruitment

On the SE aspect, there were very few fir seedlings and saplings and these plots contained a dense bamboo cover (Table 1). This is likely to be because of habitat difference (Lv and Zhang 2012) between SW and NE aspects. In the Wanglang Natural Reserve, relatively warmer and wetter micro-climate of the SE aspect are more advantageous to growth for *Fargesia denudata* than that in NE aspect (Wang and Ma 1993). In particular, competition with the abundant cover of understory bamboo (*F. denudata*) was likely to be responsible for the low frequency of seedling establishment (Dang *et al.* 2009a). Bamboos have a strong inhibitory effect on tree regeneration when they achieve a high degree of dominance in temperate forests (Taylor and Qin 1988). Taylor *et al.* (2006) have shown little regeneration of *A. faxoniana* on forest floors dominated by bamboos in the Wanglang Nature Reserve. Some studies have also demonstrated that bamboos with a relatively high cover impede tree establishment in other subalpine forests (Taylor and Qin 1992; Takahashi 1997; Holz and Veblen 2006). In addition to bamboo, competition with other species (especially *Betula* spp.) was also more prevalent in the SE plots because of the higher density of other tree species (>5-cm classes) present (Fig. 3). The density of early successional *Betula* increases with dense bamboos and late successional *Abies* decline in *Abies*–*Betula* forests in south-western China (Taylor *et al.* 2004).

Summary

The monthly mean temperature of the previous growing season and January precipitation were the dominant factors determining *A. faxoniana* growth rates along an altitudinal gradient for both the NW- and SE-facing plots in the Wanglang Natural Reserve. Precipitation during the current growing season was found to influence growth rate only at the two lowest elevations. Infrequent small-scale disturbances were not the main limiting factor for

recent fir recruitment at any site. Plots with a NW aspect contained less bamboo, and consequently recent recruitment has benefited from the high spring–summer temperature. In contrast, in plots having a SE aspect, competition from dense bamboos and other tree species greatly restricted recruitment.

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