Age structure and regeneration of subalpine fir (Abies fargesii) forests across an altitudinal range in the Qinling Mountains, China

Haishan Dang, Yanjun Zhang, Kerong Zhang, Mingxi Jiang, Quanfa Zhang *

Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, the Chinese Academy of Sciences, Wuhan 430074, PR China

1. Introduction

Forest dynamics, such as population age structure and recruitment pattern, are influenced by many factors including disturbance, competitive interactions between trees (Taylor et al., 1996; North et al., 2004). Disturbances drive the regeneration dynamics of most closed-canopy forests by creating opportunities for the establishment of new individuals through canopy opening and have been shown to play an important role in age structure and regeneration dynamics of many subalpine forests (Veblen et al., 1981; Taylor et al., 1996; Cullen et al., 2001; Parish and Antos, 2004). Community response to disturbance varies widely and depends on the types, size, severity, and frequency of disturbance and species’ life history attributes. Studies on stand dynamics can provide a substantial information on the regeneration and population structure of forests (Nakashizuka, 1991; Taylor et al., 1996; Antos and Parish, 2002).

Studies on regeneration dynamics in many forests have typically dealt with the age and size structures and seedling density (Taylor and Qin, 1988; Taylor et al., 1996; Antos and Parish, 2002; Goldblum and Rigg, 2002; Parish and Antos, 2004; Wang et al., 2004; Wangda and Ohsawa, 2006; Penuelas et al., 2007; Fyllas et al., 2008). Age structure and regeneration dynamics can be used to infer population response to known environmental events and reconstruct forest development history (Brubaker, 1986). Investigations of age structure and regeneration dynamics could give insights into the processes that determine population structure and pattern over time (Veblen et al., 1980; Svensson and Jeglum, 2001). Quantitative reconstructions of population age structure (i.e., the distribution and range of tree ages) could serve as a reference central to restoration and management of forest ecosystems (Covington et al., 1997; Fulé et al., 1997; Mast et al., 1999; Wang et al., 2004). Assessing and analyzing age structure and regeneration dynamics are therefore essential to understand the long-term ecological processes of natural forests.

Within the geographical range of a species, environmental conditions vary along physiographic and ecological gradients, creating the potential for spatial heterogeneity in growth-limiting factors and in tree establishment and regeneration (Block and Treter, 2001; Peterson et al., 2002; Carrer et al., 2007; Penuelas et al., 2007). Some environmental factors often become limiting factors resulting in poor establishment of plant individuals and insufficient recruitment of the local population. Across a species distributional range, however, optimal environmental conditions could enable a well-developed population (Taylor and Qin, 1988; Block and Treter, 2001; Wang et al., 2004; Holz et al., 2006). As a
result, age structure and regeneration dynamics of plant population, especially those with long-lived species, could act as an indicator of environmental changes across the distributional range. In the subalpine region, environmental conditions differ greatly with altitude, thus, the limiting factors related to seedling establishment and tree recruitment might vary with changes in altitude (Block and Treter, 2001; Wangda and Ohsawa, 2006; Penuelas et al., 2007). The understanding of environmental influences on population structure and regeneration dynamics of the natural forests could be improved by studies that sample across the distributional range from extreme to moderate environmental conditions (Veblen, 1989; Wang et al., 2004; Wangda and Ohsawa, 2006; Penuelas et al., 2007; Lingua et al., 2008).

The forest of subalpine fir, *Abies fargesii*, is one of the most important vegetations in the biodiversity hotspot Qinba Mountains (including the Qinling Mountains and the Daba Mountains), China. The subalpine fir forests occur over a wide elevation range above 2300 m in the Qinling Mountains, and have been undisturbed by human activities for more than a century due to relatively difficult accessibility (Zhang, 1989). However, very little is known about the age structure and regeneration dynamics of the subalpine fir forests across the altitudinal range. An understanding of age structure and regeneration patterns over the past 200–300 years would provide a context to interpret present patterns of tree establishment, and this type of ecological knowledge is fundamental for conservation and sustainable utilization of the mountain ecosystems (Cullen et al., 2001; Antos and Parish, 2002; Goldblum and Rigg, 2002; Wangda and Ohsawa, 2006).

In this study, age structure and regeneration pattern of the subalpine fir forest were examined by ageing trees and dating periods of past tree establishment across an altitudinal range, including upper limits, interior forest areas, and lower limits of the subalpine fir forest, in both the north and south aspects of the Qinling Mountains, China. The objectives of this study are (1) to reconstruct the age and regeneration structure of the subalpine fir along an altitudinal gradient; (2) to examine the differences of its age structure and regeneration pattern across the altitudinal range in the north and south aspects; and (3) to evaluate the feasibility of using age structure and regeneration pattern across an altitudinal gradient to identify forest dynamics related to environmental changes.

2. Methods

2.1. Study area

This study was conducted in the Foping and Zhouzhi National Nature Reserves (33°33′–33°57′N; 107°39′–108°19′E), located respectively in the north and south aspects of the Qinling Mountains of Shaanxi Province, China (Fig. 1). The Qinling Mountains run east-west and form an important watershed divider between China’s two great rivers, the Yangtze and the Yellow River. The Qinling Mountains are situated in the transitional zone between two macroclimatic regimes (i.e., subtropical and warm-temperate zones), making it a biologically rich area and sensitive to climatic change in China (Chen, 1983; Yan, 2006; Dang et al., 2007). Elevation in the study area ranges from 980 to 2900 m a.s.l. The south-facing slope is of subtropical characteristics with wet summers and warm winters, while the north-facing slope belongs to warm-temperate zone with relatively dry summers and cold winters. Annual precipitation ranges from 950 to 1200 mm, most of which falls between July and September. Snow cover usually lasts 5 or more months (from November to March), and annual mean temperature ranges from 6 to 11 °C below 2000 m and from 1 to 6 °C above 2000 m a.s.l. (Chen, 1983).

The natural vegetation types are deciduous broad-leaved forests (below 1800 m), mixed conifer and deciduous forests (1800–2300 m), conifer forests dominated by *A. fargesii* (2300–2800 m) and subalpine meadow (above 2800 m) along the altitudinal gradient in the study area. Umbrella bamboo (*Fargesia qinlingensis*) is a common understory species above 2300 m. The

Fig. 1. Locations of the study sites (▲) in the Qinling Mountains of Shaanxi Province, China. NL, lower distribution limit in the north aspect; NM, middle distribution zone in the north aspect; NU, upper distribution limit in the north aspect; SL, lower distribution limit in the south aspect; SM, middle distribution zone in the south aspect; SU, upper distribution limit in the south aspect.
Table 1
Species composition of the subalpine fir (Abies fargesii) forests in the Qinling Mountains, China.

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stems/ha)</th>
<th>Dominance (m²/ha)</th>
<th>Relative frequency</th>
<th>Relative density</th>
<th>Relative dominance</th>
<th>Importance value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. fargesii</td>
<td>317.5</td>
<td>40.85</td>
<td>22.73</td>
<td>61.06</td>
<td>59.80</td>
<td>47.86</td>
</tr>
<tr>
<td>Betula albo-sinensis</td>
<td>115.0</td>
<td>12.75</td>
<td>18.18</td>
<td>22.12</td>
<td>18.67</td>
<td>19.66</td>
</tr>
<tr>
<td>Acer maximowiczii</td>
<td>22.5</td>
<td>6.44</td>
<td>13.64</td>
<td>4.33</td>
<td>9.43</td>
<td>9.13</td>
</tr>
<tr>
<td>Maddenia hyxoxantha</td>
<td>17.5</td>
<td>5.76</td>
<td>11.36</td>
<td>3.37</td>
<td>8.44</td>
<td>7.72</td>
</tr>
<tr>
<td>Crataegus kansuensis</td>
<td>12.5</td>
<td>0.27</td>
<td>9.09</td>
<td>2.40</td>
<td>0.40</td>
<td>3.96</td>
</tr>
<tr>
<td>Abelia macroptera</td>
<td>7.5</td>
<td>0.04</td>
<td>6.82</td>
<td>1.44</td>
<td>0.06</td>
<td>2.77</td>
</tr>
<tr>
<td>Sorbus koehneana</td>
<td>5.0</td>
<td>0.03</td>
<td>4.55</td>
<td>0.96</td>
<td>0.04</td>
<td>1.85</td>
</tr>
<tr>
<td>Corylus tibetica</td>
<td>2.5</td>
<td>0.01</td>
<td>2.27</td>
<td>0.48</td>
<td>0.02</td>
<td>0.92</td>
</tr>
<tr>
<td>Totals</td>
<td>520.0</td>
<td>68.31</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

Table 2
Main characteristics of A. fargesii population at the different altitudinal sites in the north and south aspects of the Qinling Mountains, China.

<table>
<thead>
<tr>
<th>Altitudinal site</th>
<th>Elevation (m)</th>
<th>DBH (cm)</th>
<th>Basal area (m²/ha)</th>
<th>Density (stems/ha)</th>
<th>Canopy coverage (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>North aspect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower limit</td>
<td>2300–2400</td>
<td>41.0 ± 2.1 (66.9)a</td>
<td>28.9 ± 7.3a</td>
<td>265 ± 45.4a</td>
<td>43.4 ± 8.8a</td>
</tr>
<tr>
<td>Middle elevation</td>
<td>2400–2700</td>
<td>35.1 ± 1.7 (51.6)b</td>
<td>38.8 ± 6.9b</td>
<td>375 ± 72.8ab</td>
<td>53.8 ± 9.9b</td>
</tr>
<tr>
<td>Upper limit</td>
<td>2700–2800</td>
<td>21.3 ± 3.9 (35.1)c</td>
<td>21.1 ± 6.8a</td>
<td>470 ± 218.9b</td>
<td>48.8 ± 9.7ab</td>
</tr>
<tr>
<td>South aspect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower limit</td>
<td>2300–2400</td>
<td>40.8 ± 12.0 (63.1)a</td>
<td>29.9 ± 12.4a</td>
<td>225 ± 58.6a</td>
<td>49.6 ± 6.7a</td>
</tr>
<tr>
<td>Middle elevation</td>
<td>2400–2650</td>
<td>33.7 ± 3.6 (52.9)a</td>
<td>44.9 ± 8.4b</td>
<td>418 ± 94.4ab</td>
<td>59.8 ± 4.4a</td>
</tr>
<tr>
<td>Upper limit</td>
<td>2650–2750</td>
<td>20.4 ± 5.2 (39.5)b</td>
<td>23.1 ± 13.2a</td>
<td>535 ± 329.6b</td>
<td>53.6 ± 4.3a</td>
</tr>
</tbody>
</table>

Note: Data are presented in mean ± S.E. The values of maximum DBH are given in parentheses. The different letters indicate the significance at P ≤ 0.05 level.

research focuses on the conifer forests dominated by A. fargesii, i.e., above the elevation of 2300 m. Besides A. fargesii, the subalpine fir forests are comprised of other eight species (Table 1), each of which only has a low relative abundance (Dang et al., 2009). Historically, the subalpine fir forests in the Qinling Mountains were selectively cut several times during the period 1790–1870 (Zhang, 1989; Dang et al., 2009). In the past century, however, human activities are rare in the subalpine forest areas of the Qinling Mountains due to the relatively difficult accessibility, and some of the only remaining intact forests occur in the region (Liu et al., 2002). Thus, the study only examines regeneration dynamics of A. fargesii based on its population structure and seedling/sapling density across its altitudinal range in the Qinling Mountains, China.

2.2. Field sampling

In the summer of 2005, we measured age structure and regeneration dynamics in the deciduous to conifer forests transitional zone at the lower elevation, the interior forests dominated by A. fargesii at the middle elevation, and the treeline environment at the upper elevation in both the north and south aspects of the Qinling Mountains by sampling five plots (20 m × 20 m) at each elevation zone (Table 2). The plots were selected based on the criteria that there were similar habitats and that the stands should represent the fir forest structure at each altitudinal site. Within each plot, the DBH (diameter at breast height, 1.37 m above ground level) of each fir tree was measured, and fir trees taller than 2 m were cored at breast height. One sound core per tree was extracted in the direction parallel to the slope contour using increment borers. In total, 412 fir trees were cored. Within each plot, five 5 m² subplots were established to determine seedling (<0.5 m in height) and sapling (0.5–2 m in height) density. Thirty-eight saplings and seedlings with normal growth form were destructively sampled to create an age–height regression to estimate the time to reach breast height. Shade-tolerant species can vary greatly in growth rate, and some species of Abies can form seedling banks in which individuals can persist for a very long period (Antos et al., 2005). As a result, fir seedlings and saplings with severe release or suppression events (Nowacki and Abrams, 1997) were excluded from developing age–height regression.

2.3. Data analyses

The increment cores were dried, mounted and sanded using progressively finer sandpaper until growth ring boundaries were clearly visible. The ages of cores were read using the WinDendro image-analysis system (Regent instruments Inc., Quebec, Canada), and then crossdated by the program COFECHA (Holmes, 1983). For the increment cores missing the pith, the number of rings required to reach the pith was estimated geometrically (Dunn, 1989; Szeicz and Macdonald, 1995).

The correlation between age (y, year) and height (x, cm) of the fir seedlings is statistically significant (y = 0.2374x + 3.274, R² = 0.9335, P < 0.0001, n = 38) (Fig. 2), and it takes the fir trees about 36 years to reach breast height. Due to the absence of fir seedlings and saplings at the mid- and low-elevations, the age–height regression developed at the upper limits was used to adjust fir ages for all the sites. Ages of individual fir trees were estimated by adding the number of 36 rings on each core, the estimated age for a very long period (Antos et al., 2005). As a result, fir seedlings and saplings with severe release or suppression events (Nowacki and Abrams, 1997) were excluded from developing age–height regression.

Fig. 2. Correlations between age and height of fir seedling/sapling (<2 m in height) in the Qinling Mountains, China.
number of years for a fir to reach coring height. The age distribution was presented at 10-year interval to eliminate possible errors in the age determination process, and all the trees were also grouped into size classes at 5 cm intervals according to DBH in each site. The cross-sectional area at breast height (BA, cm²) was calculated using the DBH data. ANOVAs and post-hoc Tukey HSD tests were applied to test differences in basal area, tree density and age structure of fir populations (not including the seedlings and saplings) at the three different altitudinal sites in both the north and south aspects.

3. Results

3.1. Subalpine fir forest structure

Basal area, tree density, canopy coverage and DBH varied among the three different sites in both the north and south aspects (Table 2). The fir population at the mid-elevations in both aspects had the largest basal area and canopy coverage. A. fargesii density increased with the increase in elevation, and the fir population at the upper limits had significantly higher density than that at the lower limits in both aspects (ANOVA, \( P < 0.05 \)). DBH declined with increasing elevation, and DBH was significantly greater at lower limits than at upper limits in both aspects (ANOVA, \( P < 0.05 \)) (Table 2).

3.2. Size structure

The fir population showed a bell-shaped size distribution pattern (5-cm DBH classes) at each elevation (i.e., lower limit, middle elevation, and the treeline environment) in both aspects (Fig. 3). At the lower limits, however, large fir trees with DBH > 40 cm accounted respectively for 71.1% and 73.3% of the total fir trees in the north and south aspect, while small fir trees were rare and no fir trees with DBH < 15 cm were found. At the middle elevations, A. fargesii mainly occurred in the middle diameter classes from 25 to 45 cm. The smaller and the larger DBH classes had only small fractions of the total individuals. At the upper limits, small fir trees with DBH < 15 cm accounted, respectively, for over 22% and 21% in the north and south aspect, while no fir trees were represented in the large diameter classes more than 35 and 40 cm in the north and south aspect, respectively. In addition, the size distribution pattern indicated that large fir trees with DBH greater than 40 cm gradually decreased, and small fir trees with DBH less than 40 cm increased with increasing altitude in both aspects (Fig. 3).

3.3. Age structure

At the lower limits of both aspects, almost all the fir trees were over 120 years old (Fig. 4), and the oldest individual was more than 300 and 230 years in the north and south aspect, respectively. At the mid-elevations, the majority of the fir trees were between 110 and 170 years old. Those individuals that exceeded 200 years old were scarce, and only a few fir trees were younger than 100 years old. At the upper limits, however, most of the fir trees were between 60 and 150 years old, and 13.8% and 13.1% of fir trees were younger than 60 years in the north and south aspect, respectively (Fig. 4).

Age structure analysis indicated that fir trees' mean age decreased with the increase in elevation in both aspects (Table 3), and the fir trees at the upper limits were significantly younger than those at the lower elevations (ANOVA, \( P < 0.05 \)). Age structure distribution was similar to that for the size distribution of the fir population, displaying a decrease in the number of mature fir trees and an increase in the number of young fir trees along the altitudinal gradient in both aspects of the Qinling Mountains (Figs. 3 and 4).

3.4. Regeneration dynamics

The fir populations at the low- and mid-elevations demonstrated a unimodal regeneration type, while there was a sustained...

Fig. 3. Size class distribution of the fir trees at different elevations in the north aspect (a) and south aspect (b) of the Qinling Mountains, China.
regeneration of fir tree during the last 150 years at the upper limits in both aspects (Fig. 4). In the north aspect, there was a broad period of stem recruitment with two weak peaks during 1900–1950 and 1840–1880 at the upper limit. At the low- and mid-elevations, the majority of the fir trees were recruited from 1830 to 1890, and none during the last century (Fig. 4(a)). In the south aspect, the highest establishment occurred during the period 1860–1900, followed by lower and decreasing establishment in the last 100 years at the upper limit. There had been consistent regenerations of fir trees during the 19th century at the middle elevation and the lower limit, but no regeneration of fir trees occurred at the lower limit during the 20th century (Fig. 4(b)). The regeneration reconstruction in both aspects, however, did not include the past four decades because the breast height cores were taken. In addition, fir seedlings and saplings with a density of 1200 and 900 stems/ha for the north and south aspect were recorded at the treeline environments, but none at the low- and mid-elevations in both aspects (Table 3).

### Table 3

<table>
<thead>
<tr>
<th>Altitudinal site</th>
<th>Elevation (m)</th>
<th>Mean age (year)</th>
<th>S.D.</th>
<th>Range (year)</th>
<th>Seedling and sapling (no./ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>North aspect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower limit</td>
<td>2300–2400</td>
<td>162.11a</td>
<td>34.28</td>
<td>121–302</td>
<td>0a</td>
</tr>
<tr>
<td>Middle elevation</td>
<td>2400–2700</td>
<td>149.11a</td>
<td>24.79</td>
<td>108–182</td>
<td>0a</td>
</tr>
<tr>
<td>Upper limit</td>
<td>2700–2800</td>
<td>127.88b</td>
<td>38.48</td>
<td>43–203</td>
<td>1200b</td>
</tr>
<tr>
<td>South aspect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower limit</td>
<td>2300–2400</td>
<td>165.05a</td>
<td>32.97</td>
<td>105–239</td>
<td>0a</td>
</tr>
<tr>
<td>Middle elevation</td>
<td>2400–2650</td>
<td>134.88b</td>
<td>26.65</td>
<td>66–214</td>
<td>0a</td>
</tr>
<tr>
<td>Upper limit</td>
<td>2650–2750</td>
<td>108.70c</td>
<td>37.55</td>
<td>32–222</td>
<td>900b</td>
</tr>
</tbody>
</table>

Note: The different letters indicate the significance at $P < 0.05$ level.

### 4. Discussion

Population dynamics of plant species, especially those with long lifespan, could be considered as an indicator of vegetation dynamics as well as environmental changes across their distributional ranges (Brubaker, 1986; Wang et al., 2004; Camarero et al., 2005). The long lifespan of trees makes it infeasible to witness their whole life history, so a static investigation on age structure and regeneration of population is often accepted in population dynamics estimates (Brubaker, 1986; Svensson and Jeglum, 2001; Wangda and Ohsawa, 2006). However, care must be taken when explaining static age structure data because of differences in species mortality with various age and stand-history events.

Interpretation of tree population dynamics requires information on the temporal patterns of tree establishment, often inferred from age and size distributions (Cullen et al., 2001). Age and size studies along an altitudinal gradient are helpful for understanding the relationship between environmental factors and population dynamics.
dynamics. An upsurge in tree recruitment and establishment coupled with increase in tree density is often an indication of regeneration response to changes in environmental and/or climatic conditions (Harcombe, 1987; Motta and Nola, 2001; Penuelas et al., 2007). In this survey of population structure, the distribution of individuals over the range of tree sizes might represent the change in the rate of fir tree regeneration over time across the altitudinal range in the Qinling Mountains.

The Qinling Mountain range constitutes a critical boundary for climate and vegetation distribution in eastern central mainland China owing to its importance as a geographic demarcation line. Although climate conditions between the southern and northern slopes are quite different (Yan, 2006), the dynamics of the fir regeneration showed no significant differences between the north and south aspects (Fig. 4). Climatic conditions show large spatial variations in mountainous areas, while the microclimatology of montane landscapes is dependent on latitude, continentality and topography (Barry, 1992). In this study, the sampling location in the north aspect is F. qinlingensis, and the south aspect within a small geographical region (Fig. 1), which might be responsible for the similar fir regeneration dynamics in both aspects.

Low temperature at the upper treeline ecotones could inhibit tree growth and development, while low precipitation and low soil moisture at the low-elevations might also restrict tree growth and development (Whittaker, 1956; Block and Treter, 2001). At the mid-elevation distributional area of a woody population, which provides relatively more suitable environmental conditions, the intrinsic biological traits of the tree species rather than environmental factors would play a larger role in the structure and regeneration dynamics of the population (Wang et al., 2004).

Age structure and size distribution of long-lived tree populations growing under near optimum conditions often show a reverse-J-shape due to the initially high mortality of juvenile trees in the smallest size class (Svensson and Jeglum, 2001; Penuelas et al., 2007). In this study, however, the fir populations at the low- and mid-elevations demonstrated a unimodal regeneration type (Figs. 3 and 4). This size and age structure is probably indicative of the impacts of past disturbances (such as unfavorable climate, pest and pathogen outbreak, intensive understory cover) with peak presumably corresponding to periods of high recruitment after disturbance (Taylor and Qin, 1988; Penuelas et al., 2007). In most subalpine forests, age structure and regeneration dynamics of a plant population can be influence by many factors such as disturbance and climatic and environmental conditions (Brubaker, 1986; Antos and Parish, 2002; Parish and Antos, 2004, 2006; Wang et al., 2004), and a distinct pulse of tree establishment evident in an age-class distribution often an indication of regeneration in response to canopy-opening disturbance (Cullen et al., 2001; Parish and Antos, 2004).

Disturbances are common in subalpine forests and they influence community structure and dynamics (Taylor et al., 1996). Natural disturbances drive the regeneration dynamics of most closed-canopy forests by creating opportunities for the establishment of new individuals through canopy opening and have been shown to play a role in the regeneration dynamics (Yebleton et al., 1981; Cullen et al., 2001). In the study region, the subalpine fir forests were selectively cut several times during the time period from the 1790s to 1870s (Zhang, 1989; Dang et al., 2009), leading to the recruitment pulse of the fir trees from 1830 to 1890 across the altitudinal range (Fig. 4). Disturbance agents such as fire and livestock grazing that have played an important role in tree regeneration (Vale, 1981; Elliot and Baker, 2004) are absent in the Qinling Mountains (Wang, 1961), and previous research has illustrated that the F. fargesii forest experienced frequent small-scale disturbances and few large-scale disturbances (i.e., selective cutting from the 1790s to 1870s) in its development history (Dang et al., 2009).

The absence of fir seedlings and saplings and low recruitment of fir tree in the last century at the lower limits and mid-elevations in both aspects (Fig. 4) might be attributed to the influences of understory bamboo (F. qinlingensis) on recruitment success (Taylor and Qin, 1988; Nakashizuka, 1991; Wang et al., 2006; Dang et al., 2007). Bamboos, which are common understory plants in the temperate and tropical subalpine forests, appear particularly effective in reducing seedling recruitment and tree regeneration when they achieve a high degree of dominance (Taylor and Qin, 1988; Taylor et al., 1996; Narukawa and Yamamoto, 2002; Holz et al., 2006). At the lower limits and mid-elevations in the study region, the understory bamboo with a height of 1.5–3.0 m and a density of 70–140 stems/m², usually covers more than 85%, sometimes 100% of the understory of the subalpine fir forest (Ren, 1998; Wang et al., 2006). The lack of fir recruitment at the lower limits and mid-elevations is likely to be linked to intensive cover of bamboos, which limited germination and seedling survival and development in the last century in the Qinling Mountains (Taylor and Qin, 1988; Dang et al., 2007), which is similar to other subalpine forests in China, Japan and South America (Taylor and Qin, 1988; Nakashizuka, 1991; Narukawa and Yamamoto, 2002; Holz et al., 2006). Like most other bamboos in tropical and temperate regions, F. qinlingensis is also a perennial monocarpic species which is known for its long period of vegetative growth followed by mast seeding, and it flowers ca. every 50 years (Taylor and Qin, 1988; Wang et al., 2006). In the subalpine fir forests of western China, the coexisting species, such as Betula spp., preferred different seed-beds than Abies for establishment and regeneration, and seedlings of the coexisting species established more frequently on raised surfaces than Abies (Taylor et al., 2006). This led to more successful regeneration of coexisting species than Abies on raised surfaces and little regeneration of Abies on the forest floor which was occupied by bamboo (Taylor and Qin, 1988; Taylor et al., 2006). Without large-scale disturbances such as fire or bamboo mass-flowering to reduce the intensity of the understory bamboo in the future, very little opportunity will exist for recruitment in the subalpine fir forests at the low- and mid-elevations in the Qinling Mountains (Wang et al., 2006).

At the upper limits in both aspects, a large number of stem recruitment occurred during the last century (Table 2; Fig. 4). This might be partly due to the lower level of the understory bamboo cover at the upper limits in the subalpine regions (Taylor and Qin, 1988; Taylor et al., 1996; Ren, 1998; Holz et al., 2006). However, the lack of stems that were recruited after 1960 at the upper limits is partly an artifact of not coring young stems <2 m in height that would likely occupy the <40 years age classes (Fig. 4). Hence it appears that there was an upsurge in stem recruitment in the period 1850–1960 that has not been sustained in recent decades at the upper limits in both aspects.

Apart from the reduction in intensity of the understory bamboo (F. qinlingensis), climatic variability might also play an important role in the age structure and regeneration dynamics of the fir populations at the upper limits (Camarero and Gutierrez, 1999; Daniels and Veblen, 2004; Penuelas et al., 2007). Tree populations at altitudinal treeline ecotones, where low temperature limits tree regeneration and growth, are considered to be very sensitive to climate warming. The age structure and regeneration dynamics of trees at subalpine treelines can reflect the dynamics (e.g., shift or invasion of species) in relation to climate change and variability (Payette and Filion, 1985). Many studies have demonstrated that upper treelines often respond to climate warming with increases in recruitment and tree density as well as upward advances over the last 50–100 years (Payette and Filion, 1985; Rochefort et al., 1994;
A seedling bank of long-lived subalpine fir appears critical to the dynamics of the subalpine forests, because it can be the major source of new canopy trees following mortality from disturbances such as windthrow or insect outbreaks (Parish and Antos, 2006). The sustained establishment of fir seedling at the upper limits might promote variations in stand structure and regeneration dynamics of the subalpine fir forests along the altitudinal gradient in the Qinling Mountains, China.

5. Conclusions

Age structure analysis showed a unimodal age structure of the fir population at low- and mid-elevations, indicating that environmental factors might play an important role in shaping its age structure and regeneration dynamics at those sites. Fir regeneration dynamics in the north aspect were similar to those in the south aspect. The majority of the subalpine fir trees were recruited into the forest in the time period 1830–1890 at each altitudinal site, which might be triggered by selective cutting events from the 1790s to 1870s. At the low- and mid-elevations, however, there were no fir seedlings and saplings, and no stem recruitment occurred in the last century, which might probably be attributed to the influence of the dense cover of understory bamboo on seedling establishment. At the upper limits, sustained fir recruitment was found in the last 150 years, and seedlings and saplings with a density of 1200 and 900 stems/ha in the north and south aspect were also recorded in the recent decades, leading to the significant increase in tree density at the treeline ecotones. The sustained fir seedling establishment at the upper limits would probably result in variations in stand structure and regeneration dynamics of the subalpine fir forests along the altitudinal gradient in the Qinling Mountains, China.

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References


Narukawa, Y., Yamamoto, S., 2002. Effects of dwarf bamboo (Sasa sp.) and forest floor microsites on conifer seedling recruitment in a subalpine forest area. For. Ecol. Manage. 163, 61–70.


