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Age structure of *Picea schrenkiana* forest along an altitudinal gradient in the central Tianshan Mountains, northwestern China

Ting Wang[a,b], Yu Liang[b], Haibao Ren[b], Dan Yu[a], Jian Ni[b], Keping Ma[b,*]

[a]College of Life Science, Wuhan University, Wuhan 430072, PR China
[b]Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, PR China

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Abstract

Size distribution and age structure of Schrenk spruce (*Picea schrenkiana* Fisch. et Mey.) forest along the altitudinal gradient on the central Tianshan Mountains was studied in this paper. The forest was divided into three transects, i.e., lower limit (1500–1700 m), mid-altitude (1800–2400 m) and upper limit (2500–2700 m). Age of each individual was estimated by the age–height relationships of seedlings or saplings and the age–DBH (diameter at breast height) relationships of big trees. A reverse-J shape age structure was found in the mid-altitude transect; the age structure of the low altitude transect was characterised by the dominance of young trees, whereas the transect of high altitude lack of young seedlings and saplings. It is implied that different limiting factors play important roles in shaping the age structure and regeneration of forest at different altitudes. In the mid-altitudinal transect, density dependent competition between trees is probably the most important influencing factor. We propose that limiting environmental factors, e.g. temperature and precipitation, play important roles in determining the age structure of *P. schrenkiana* population in the high or low limit transacts.

Keywords: Age classes; Altitudinal transect; Treeline

1. Introduction

Population dynamics of plant species, especially those of long-lived species, could be considered as an indicator of vegetation succession as well as climate changes on treeline ecotone (Brubaker, 1986; Camarero and Gutiérrez, 2004). As it is generally infeasible to trace the whole life history, from birth to death, of a long-lived species, a static investigation on age structure of population was often accepted in population dynamic estimations (Harper, 1977; Stewart, 1986; Johnson and Fryer, 1989; Svensson and Jeglum, 2001).

Age structure investigations could give insights into the processes determining population structure over time (Stewart, 1986; Johnson and Fryer, 1989; Svensson and Jeglum, 2001). Quantitative reconstructions of age structure conditions (the distribution and range of tree ages), could also serve as a basic point of reference central to restoration and management of forest ecosystems (Covington et al., 1997; Fulé et al., 1997; Mast et al., 1999). Assessing and analysing age structures are therefore prerequisites for understanding ecological processes and restoration of natural forests.

Plant could generally grow and survive in certain range of environmental gradients, e.g. temperature,

* Corresponding author. Tel.: +86-10-62591431x6223; fax: +86-10-62590833.
E-mail address: makp@brim.ac.cn (K. Ma).

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precipitation (Block and Treter, 2001). Optimal environmental conditions could enable a well-developed population and limiting factors would result in poor growth of plant individuals as well as problems in the regeneration process of the local population. It is also well documented that environmental factors influence the regeneration of plants, e.g. drought, waterlogging, high or low temperature, could also affect the age structure of plants (Block and Treter, 2001). Age structures of plant populations, especially those of long-lived species, could therefore act as an indicator of environmental changes.

Environmental gradients were often found along altitude gradient of mountains, and the distribution of a plant species could indicate the adaptability of the plant to environment. On the edge of the distribution area of a plant population, e.g. treelines on a mountain, some environmental factors often become limiting factors inhibiting the expansion of the population (Block and Treter, 2001). Age structure studies along an altitude gradient of a mountain would be helpful in understanding the influences of environmental factors on the regeneration of natural forests.

The forest of Schrenk spruce, *Picea schrenkiana* Fisch. et Mey., is one of the most important zonal vegetations in the arid land of Xinjiang Uygur Autonomous Region, northwest of China. The *P. schrenkiana* population in our study distributed from 1500 to 2700 m a.s.l. on the central Tianshan Mountain (Zhang and Tang, 1989).

The whole forest was divided into three transects, i.e. lower limit (1500–1700 m), upper limit (2500–2700 m), and mid-altitude forest (1800–2400 m). Age structures of three transects in the Schrenk spruce forest were compared in this paper and the objectives are: (1) to find the differences of age structure along an altitude gradient; (2) to evaluate the possibility of using age structure assays in environmental change studies.

2. Methods

2.1. Study area

The study was conducted in the Tianchi Natural Reserve in central Xinjiang Uygur Autonomous Region, northwest of China (88°00′–88°20′E, 43°45′–43°59′N). The mean annual precipitation is 400–500 mm and the mean annual temperature is 2.04 °C in the studied area. The mean annual non-frost period is 88.6 days, and the mean relative humidity is 56–64% (climate data were provided by Tianchi weather station, 1935 m a.s.l.).

The dominant species of the study area is *P. schrenkiana*, and *Populus tremula*, *Sorbus tianschanica*, *Salix xerophila*, *Betula tianschanica*, *B. verrucosa*, and *B. microphylla* are also companion species in the forest. Soil type of the study site is mountain grey-brown forest soil (Zhang and Tang, 1989).

2.2. Field sampling

The field investigations were carried out from 2 June to 28 July 2001. Stands were selected at 100 m elevation interval from 1500 to 2700 m, and two stands (20 m × 20 m) were examined at each altitude. A total of 26 forest stands were investigated along an altitudinal gradient in the central Tianshan Mountain (Fig. 1). The stands were similar in topography and wet microsites or rock outcrops were avoided. In all stands, *P. schrenkiana* individuals were defined as trees (height (H) $\geq$2 m), saplings (0.5 m $\leq$ H $<$ 2 m), and seedlings ($H < 0.5$ m).

Ages of 100 seedlings or saplings were determined by counting branch annulus and the age–height relations were established in each transect. Height of other seedlings or saplings was also measured and the ages were calculated by the regression equations between age and height of seedlings and saplings.

The DBH of each tree was also measured in each transect and all trees were grouped into size classes according to DBH (in 5 cm diameter intervals). Forty, 89, and 51 trees were selected randomly and cored for age determining in the high-, mid-, and low-altitude transect, respectively. Regression equations between DBH and age were established in the three transects, and ages of other trees were calculated.

Three soil cores (0–30 cm) were taken randomly in each stands and soil moisture were measured.

2.3. Data processing

Some cores were discarded because of missing or rot in the centre, and only those cross the centre of trunk were used in further analysis. All cores were mounted, and then sanded with successively finer

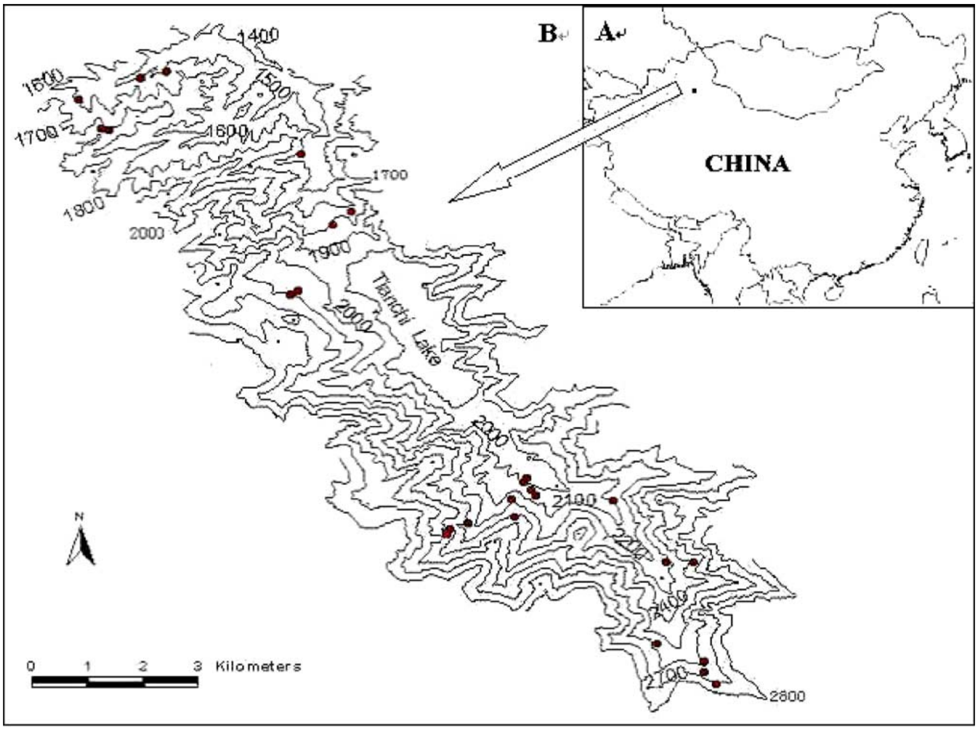

Fig. 1. Location of stands in Tianshan Mountains, northwestern China. (A) Location of study area in China. (B) Scheme of stands in Tianchi Forestry Center.

grades of sandpaper until annual rings could be easily distinguished. The age of core samples were read by the apparatus WinDENDRO™ 2001b (Université Du Québec À Chicoutimi, Canada), and then crossdated by the software COFECHA (Holmes, 1983). For better age estimation, the average age of the two cores of the same tree were accepted.

Each soil example was tare its wet weight, and then weighed its dry weight after drying in 105 °C for 12 h. The soil moisture (%) of every stand was calculated using the difference of wet and dry weights divided by the gross soil weight:

$$\text{Soil moisture}\ (\%) = \frac{\text{wet weight} - \text{dry weight (g)}}{\text{wet weight (g)}} \times 100$$

3. Results

3.1. General characteristics

Densities of seedlings/saplings, living trees, and fallen trees, as well as coverage of trees were list in Table 1. The density of seedlings and saplings was relatively low in the high-altitude transect and significant difference was found between high-altitude and mid-altitude transects ($P = 0.026$). Significant difference was also found between densities of fallen trees in low-altitude and mid-altitude transects ($P = 0.019$).

Significantly positive regression was found between soil moisture and altitude ($r = 0.83, P < 0.001$) (Fig. 2).

3.2. DBH patterns

The DBH frequency distributions of the Schrenk spruce population were quite different in different altitude transects in the present study (Fig. 3). In the low-altitude transect, small trees (DBH < 10 cm) accounted for over 70% of Schrenk spruce trees, whereas big trees were rare and no trees were found over 40 cm in DBH. In the mid-altitude transect, the smallest two classes, the 0–5 cm and the 5–10 cm DBH classes, accounted for 17.4 and 25.4% of the total trees,

Table 1
General characteristics of *P. schrenkiana* population in different altitudinal plots in the central Tianshan Mountains*

Altitude transect (m)	Seedlings and saplings (ha^{-1})	Living trees (ha^{-1})	Fallen trees (ha^{-1})	Coverage (%)
High-altitude (2500–2700)	129 ± 79b	812 ± 519a	8.0 ± 3.3ab	43.9 ± 10.2a
Mid-altitude (1800-2400)	1577 ± 467a	1109 ± 119a	7.3 ± 2.2a	59.6 ± 3.7a
Low–altitude (1500-1700)	646 ± 234ab	992 ± 308a	0 ± 0b	54.0 ± 14.4a

[*] Data are presented in mean ± S.E.

respectively. The number of individuals decreased gradually with the increasing of DBH. In the high-altitude transect, a bell shaped frequency distribution of DBH was found. The smallest and the biggest DBH classes (DBH < 5 cm and DBH ≥ 45 cm) had only small fractions of individuals (4.6 and 2.1%, respectively), whereas the 10–15 cm class accounted for 24.7% of individuals in this transects.

3.3. Age–DBH or age–H relationships

The regression equations between age and height of seedlings or saplings as well as between age and DBH of trees were listed in Table 2. All the regression equations were statistically significant ($P < 0.001$). With all the DBH data of trees and height of seedlings and saplings on the different stands, the age structures and distributions of *P. schrenkiana* forest on the different altitudinal transects could be calculated.

3.4. Age patterns

Age structures of *P. schrenkiana* forest in different transects on the central Tianshan Mountains were similar to DBH patterns (Fig. 4).

In the mid-altitude transect, a reverse-J-shaped age distribution was found. Two youngest classes, i.e. 1–10a and 10–20a classes, accounted for 36.2 and 14.9% of total individuals, respectively. Old trees were also found in this area and more than 2% individuals were over 200 years old.

Compared with the mid-altitude transect, the age structures of low-altitude and high-altitude transects were quite different. In the low altitude transect, old trees were rare and no individuals were found over 100 years old. The majority of trees in the low altitude transect (41.7%) were between 41 and 60 years old and 8.8% trees were less than 10 years old. In the high altitude transect, a bell-shaped age

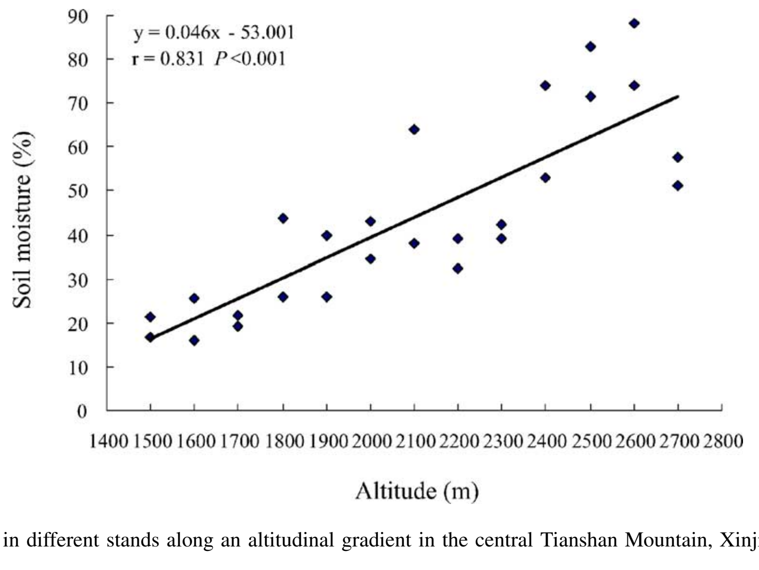

Fig. 2. Soil moisture (%) in different stands along an altitudinal gradient in the central Tianshan Mountain, Xinjiang, northwestern China.

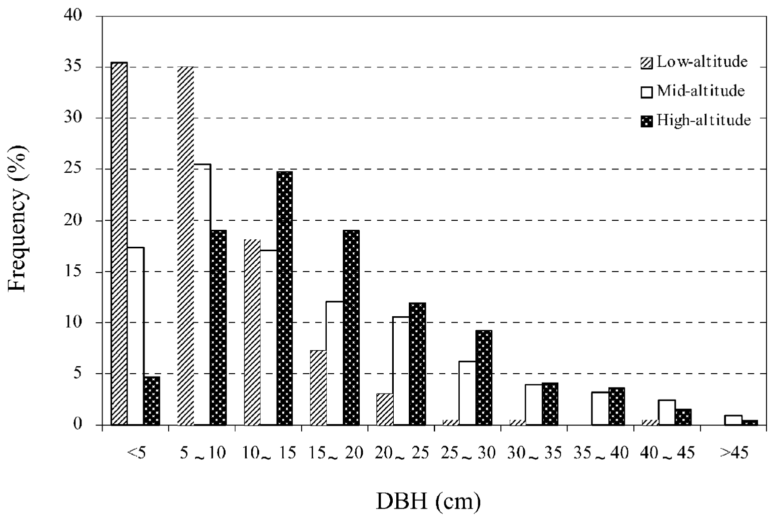

Fig. 3. The percentage distribution of DBH classes of *P. schrenkiana* population on the different altitudinal transects in the central Tianshan Mountain, Xinjiang, northwestern China.

Table 2
Regression equations between age (*A*) and DBH (*D*) for trees or between age and *H* (height) for seedlings ($H < 50$ cm) and saplings ($50\,\mathrm{cm} \leq H < 2\,\mathrm{m}$) of *P. schrenkiana* at the different altitudinal transects in the central Tianshan Mountain, Xinjiang

Transects	Seedlings ($H < 50$ cm) and saplings ($50\,\mathrm{cm} \leq H < 2\,\mathrm{m}$)	Trees ($H \geq 2$ m)
High-altitude (2500–2700 m)	$A = 0.652H^{0.838}$; $r = 0.946$; $P < 0.001$	$A = 3.184D+48.512$; $r = 0.789$; $P < 0.001$
Mid-altitude (1800–2400 m)	$A = 0.725H^{0.751}$; $r = 0.984$; $P < 0.001$	$A = 21.668D^{0.590}$; $r = 0.766$; $P < 0.001$
Low-altitude (1500–1700 m)	$A = 0.168H+2.048$; $r = 0.982$; $P < 0.001$	$A = 1.182D+34.397$; $r = 0.780$; $P < 0.001$

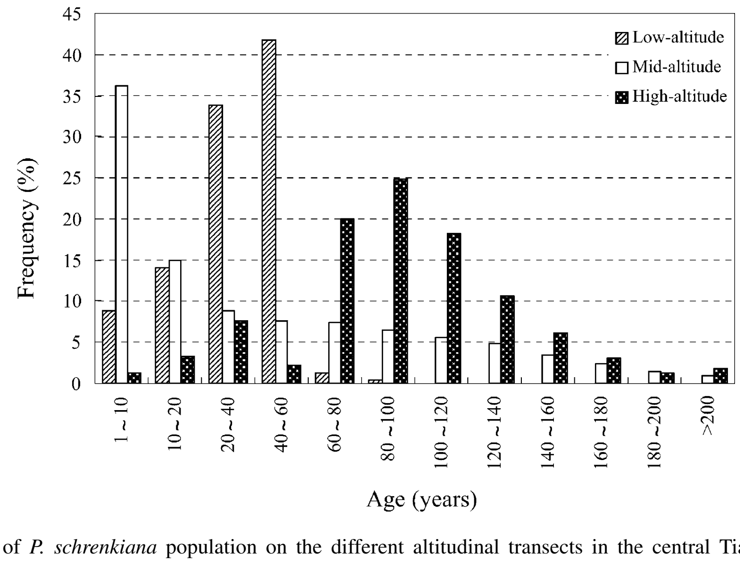

Fig. 4. The age structure of *P. schrenkiana* population on the different altitudinal transects in the central Tianshan Mountain, Xinjiang, northwestern China.

structure was found and most trees were found between 61 and 140 years old. Young individuals were rare in this transect and merely 14.2% trees were less than 60 years old.

4. Discussion

Many factors, such as seed productivity and dispersal, competition, climatic shifts, animals' feeding, pathogens, and anthropic disturbance, could influence the age structure of a plant population (Brubaker, 1986; Davis et al., 1986; Mueller-Dombois, 1987; Peet and Christensen, 1987; Stewart and Rose, 1986; Arseneault and Payette, 1997). As to a mature plant population under optimal conditions, i.e. no severe disturbances of human, pathogens and animals, the age structure will depend much on the biological traits of the objective plant species. Size distributions and age structures of long-lived tree populations were often found reverse-J-shape (e.g. Hörnberg et al., 1995; Svensson and Jeglum, 2001) due to relatively higher mortality rate of young individuals in the population (Peet and Christensen, 1987).

Environmental factors, e.g. temperature and soil moisture, generally change regularly along an altitude gradient. With the increasing of altitude, the average temperature decreases and precipitation increases. In the upper treeline on a mountain, low temperature and short growth season could inhibit growth and development of trees (Block and Treter, 2001). In the low altitude area of a mountain, on the other hand, the growth of plants is also restricted by low precipitation and low soil moisture (Block and Treter, 2001). In the middle of distributed area of a woody population, providing relatively more suitable environmental conditions, the intrinsic biological traits of the tree species rather than environmental factors would be responsible for the structure of the population. Because of density dependent competition or self-thinning of seedlings, younger individuals generally have a higher mortality rate than mature trees (Peet and Christensen, 1987). The reverse-J-shape age structure in the mid-altitude transect in the present study indicated that environmental factors had little effects on the age structures in the central distribution region of *P. schrenkiana*. And the abnormal age structures of the high-altitude and low-altitude transect may probably be due to the shifts of limiting factors, e.g. temperature and precipitation.

In the high-altitude transect, the upper limit of the forest, temperature may be the main limiting environmental factor and the changes of temperature may affect the population structure of *P. schrenkiana* greatly. Since low temperature usually does harm to seedlings and has little effects on mature trees, extremely low temperature or frequent cold waves in history would result in lack of individuals in the corresponding age classes. Better conditions in the high-altitude, on the contrary, would result in more individuals in the corresponding age classes. The age structure of high-altitude transect is therefore more sensitive to the shifts of temperature than that of mid-altitude transect. While age structure was not an accurate indicator of temperature shifts, it could still indicate the temperature changes on relatively larger time scales. The results of the present study indicated that an extremely low frequency in the 40–60a age class, which implied a period of extremely cold weather or cold episodes frequently occurrences in 1940 and 1950s. The results also indicate that more individuals were found in age classes around 90a than in classes of recent 60 years, implying that the environmental conditions of 80 years ago were more suitable for seedling survival and population regeneration in the high-altitude transect than those of recent years. It is interesting that the 1900 and 1910s seems to be warmer or having less cold waves than recent 60 years, which was not agreeing with the trends of global warming. Possible reasons are: (1) while global warming is the trends of the world weather conditions, it is still not the case in some area in the world; (2) although the average temperature tended to increase, the extreme low temperature in spring, autumn, or winter, which were more important for survival of seedlings, could still decrease; (3) the weather could be much unstable with the global warming, and there would be probably more cold waves in spring and autumn, which would do harm to growth and survival of seedlings. Based on investigations on tree-limits in north of Europe, Kullman (1996, 1998, 2001, 2003) suggested a cooler period in the past 4–5 decades, which resulted in defoliation, retarded growth, inhibited regeneration and locally some tree-limit retraction in the high-elevation forests. In a recent study, Camarero and Gutiérrez (2004) found a negative relationship between mean treeline-advance rate and

March temperature variability, they believed that if the interannual variability of March temperature increases, the probability of successful treeline ascent would decrease.

In the low-altitude transect, it was much more complex and the limiting factors included not only environmental factors (e.g. precipitation) but also competition of lower-altitude zonal vegetation (Block and Treter, 2001). Our results indicated that the *P. schrenkiana* in the low-altitude transect did not form a mature forest and most individuals established since 1940s. The thriving of *P. schrenkiana* in the low-altitude transect in recent 60 years might be due to the ameliorated precipitation conditions or alleviated competitions of other plant species. If precipitation and soil moisture increased in the low-altitude transect, more seedlings would survive in the water-limited conditions (Block and Treter, 2001). Since the low-altitude transect could also be the upper limit of other plant species, decreased temperature or increased frequency of cold waves would inhibit the growth and survival of seedlings of other trees, which would also result in thriving of *P. schrenkiana*.

While the tree ring is a more accurate indicator of environmental changes and has been applied to reconstruct past climate in many studies (e.g. Hughes et al., 1984; Briffa et al., 1990; Xiong and Palmer, 2000), the age structure could indicate different aspects of environmental conditions (Earle, 1993). The width of tree rings could indicate environmental factors affecting the growth of trees, e.g. the temperature and precipitation in the growth season (Earle, 1993; Akkemïk, 2000), whereas the age structure could indicate the environmental factors influencing the reproduction and mortality rate of individuals, e.g. extreme temperature and natural disasters. While the correlations between age structure and weather changes are not very clear, its potential application in global change estimation should also be considered. The age structure studies along altitudinal gradient will be helpful to understand the relationship between environmental factors and plant population dynamics.

Compared with optimal conditions, tree-limits have limiting climatic factors inhibiting the growth and survival of plants. Size distribution and age structure of tree-limits, correspondingly, could serve as sensitive biomonitors of climate change and variability. Studies on age structure of tree-limits, combining with information of climatic records and radial growth of trees, will be helpful in reconstruction of climate conditions in the history as well as in understanding the plant–environment interactions.

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