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Spatial Structure of Alpine Trees in Mountain Baima Xueshan on the Southeast Tibetan Plateau

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Most of the trees at treeline on the Tibetan Plateau are endemic to the Plateau. Yet little is known about these species. The study focused on the population structure, spatial patterns and associations of the treeline species *Abies forestii* var. *georgei* and *Juniperus saltuaria* at treeline and timberline in Mountain Baima Xueshan on the southeast Tibetan Plateau. These species form monodominant communities on the north- and south-facing slopes, respectively. Stem density, DBH-distribution, distribution pattern of different tree size classes, and intraspecific spatial association between different tree size classes of both species were analyzed. Spatial structure varied between *A. forestii* var. *georgei* and *J. saltuaria*, and for the same species, the spatial structures were also different from timberline to treeline. Stem density, mean tree height and young individuals of *A. forestii* var. *georgei* were significantly higher than those of *J. saltuaria*. For the same species, they were different from timberline to treeline, i.e., stem density and mean tree height of both species became lower. Size classes of both species were mainly clustered either at treeline or at timberline but at different scales, and spatial patterns of young *J. saltuaria* were mainly dominated by random patterns. Clumps of trees created more favorable micro-environments in harsh environments at treeline and timberline. Most tree size classes showed positive intraspecific spatial associations, but positive associations between size classes of *J. saltuaria* were not as significant as those of *A. forestii* var. *georgei*. The south-facing slope was usually subjected to varying intensities of pastoralism. Livestock disturbance greatly changed the microhabitat and reduced the number of young individuals. The potential of trees to regenerate was greatly inhibited, while *A. forestii* var. *georgei* showed greater regeneration potential. Spatial structures of *J. saltuaria* were also modified by this kind of human impact.

Keywords treeline, timberline, *Abies forestii* var. *georgei* (Orr) Farjon, *Juniperus saltuaria* Rehder & E.H. Wilson, spatial point pattern

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1 Introduction

Alpine treeline, the transition from forest to treeless alpine areas, represents one of the most distinct boundaries within the altitudinal zonation of vegetation and at the same time, one of the most fundamental ecological boundaries. It has attracted geographers and ecologists to do research for a long time on the phenomena it encompasses. Pioneers started systematic treeline research in the European Alps in the 1900s, and by now, profound knowledge of upper treelines in Europe, North America and New Zealand has been accumulated (Schickhoff 2006). These researchers largely contributed to our current understanding of ecological conditions and processes of the treeline ecotone. However, considerable research deficits still remain as far as treelines on other continents, especially in subtropical and tropical high mountains, are concerned.

The high mountains on the Tibetan Plateau support the highest treelines in the world, and most of the trees at treeline are species endemic to the Plateau (Sun and Zheng 1998, Miehe et al. 2006, 2008, Zhang 2007). On the southeast Tibetan Plateau, different tree species form treelines on different slopes: *Juniperus* spp. usually on south-facing slopes and *Abies* spp. on north-facing slopes, and they constitute the natural alpine coniferous forests of this area. These forests serve important water-, soil- and biodiversity-preservation functions and act as a significant ecological barrier of the regions and the upper reaches of the Yangtze River (Liu 2002). However, these important plant species have received little attention, neither basic relationships of treeline to ecological conditions nor differences between species on south- and north-facing slopes, so far.

Description of spatial pattern of plant community is a necessary step to understand its dynamics (Watt 1947). Spatial issues have interested ecologists for a long time and have been receiving increasing attention by ecologists over the last years (Chen and Bradshaw 1999, Wiegand et a1. 2000, Schurr et a1. 2004, Hao et al. 2007). Spatial point pattern analysis is commonly used to study the distribution of the horizontal space among trees within a region of interest, and its objective is to measure how individuals are located with respect to each other by using quantitative characteristics (Tomppo 1986). Quantifying such patterns will increase our ability to predict the response of the communities to both natural and anthropogenic environmental change.

We investigated the natural stands at treeline (an ecotone between closed tall forest and tree species line) and timberline (the upper limit of closed tall forest) of *Abies forestii* var. *georgei* (Pinaceae) on the north-facing slope and *Juniperus saltuaria* (Cupressaceae) on the south-facing slope of Mountain Baima Xueshan on the southeast Tibetan Plateau. We hypothesized that: Alpine trees on different slopes of Mountain Baima Xueshan showed different spatial structures; alpine trees on the same slope had different spatial structures at different elevations. Our objectives were to: 1) characterize the population structures of both species in the study area, 2) examine the spatial patterns of tree size classes and intraspecific spatial associations among different tree size classes of both species, 3) determine whether spatial structures of the two species differed with change in elevation from timberline to treeline, 4) determine whether spatial structures of trees differed on different slopes and 5) examine the processes which may have contributed to these patterns and differences.

2 Material and Methods

2.1 Study Area and the Investigated Species

The study was conducted in the alpine zone of the National Natural Reserve of Mountain Baima Xueshan (27°47´–28°36´N, 98°57´–99°21´E) in Deqin County, Yunnan province, China (Table 1). This reserve is situated on the southeast Tibetan Plateau with the total area 281 640 ha, and the highest peak 5429 m asl. and mean altitude 4000 m. Coniferous forests form the natural vegetation of this zone. The north-facing slope is dominated by *A. forestii* var. *georgei* in tree layer, *Rhododendron* spp. in shrub layer and *Carex* spp., *Kobresia* spp. and moss on the ground layer (Liu 2004). The south-facing slope is dominated by *J. saltuaria* in tree layer, *Juniperus squamata* in shrub layer and some small forbs and graminoids such as *Euphorbia stracheyi*, *Spenceria*

Table 1. Geographic, topographic and structural characteristics of the four stands studied at treeline and timberline in Mountain Baima Xueshan.

Characteristics	North-facing slope (*Abies forestii* var. *georgei*)		South-facing slope (*Juniperus saltuaria*)	
	Treeline	Timberline	Treeline	Timberline
Site characteristics				
Latitude	28°26´57˝N	28°27´01˝N	28°21´55˝N	28°21´58˝N
Longitude	98°59´40˝E	98°59´35˝E	99°02´04˝E	99°02´00˝E
Maximum treeline/timberline elevations (m asl)	4430	4388	4398	4370
Mean slope (°)	19	22	28	31
Aspect (°)	62	65	235	237
Elevation of the plot center (m asl)	4410	4378	4392	4360
Content of soil organic matter	10.12%–12.35%		7.42%–9.95%	
Soil pH	4.62–5.83		4.97–6.24	
Stand structure				
Density of living trees (ha^{-1})	708	4177	348	633
Density of seedlings (ha^{-1})	408	2933	28	-
Density of saplings (ha^{-1})	164	400	148	111
Density of adult trees (ha^{-1})	136	844	172	522
Mean height (m)	1.95	4.99	2.40	4.11
Maximum height (cm)	5.3	11.8	4.2	7.0
Maximum DBH (cm)	21.8	25.2	18.9	23.6
Basal area (m^2 ha^{-1})	10.3	27.9	6.1	11.2
Cover of tree layer (%)	20	40	15	25
Cover of shrub layer (%)	>90	40	40	15
Cover of herb layer (%)	15	25	30	20

ramalana, *Potentilla anserina*, *Potentilla saundersiana*, *Carex* spp. and *Kobresia* spp. on the ground layer.

Both *A. forestii* var. *georgei* and *J. saltuaria* are endemic to the Tibetan Plateau. *A. forestii* var. *georgei* is able to reach a height of 30 m in a closed forest. The natural distribution of *A. forestii* var. *georgei* is limited to the eastern Tibetan Plateau and it constitutes a pure forest from 3400 m to 4400 m in Mountain Baima Xueshan. In the treeline ecotone, the understory is usually covered by *Rhododendron* spp. and its coverage can reach 80–90%. With a slower growth rate, *J. saltuaria* can only reach 15 m (Fig. 1). Because of severe disturbance, especially animal grazing in the past decades, only sporadic primitive forests formed by *J. saltuaria* can be found in northwest Yunnan and Sichuan province, China. *J. saltuaria* has a great advantage in ecological restoration of high-altitude ecosystem because of its cold-, wind-, and drought-resistance characteristics.

2.2 Field Sampling

The populations were studied in June, 2005. According to the topographic conditions, one square 50 m × 50 m plot in the treeline ecotone and 30 m × 30 m at timberline, respectively, were set up for detailed survey in the south- and north-facing slopes (Table 1). The plots were placed where topography was uniform and one side of each plot was parallel to the maximum slope. Position was recorded for each individual. Point $(x, y) = (0, 0)$ of each plot was located in the lower left corner looking upslope. Current elevations of treeline and timberline were measured in the field (accuracy of ±0.1 m). Individuals were defined as trees (height (H) ≥ 2 m), saplings (0.5 m $\leq$ H < 2 m), and seedlings (H $<$ 0.5 m) (Wang et a1. 2004). Every tree inside each plot was measured for: position of the center of the tree (x and y coordinates), DBH (Diameter at Breast Height) or diameter at base for seedlings and saplings,

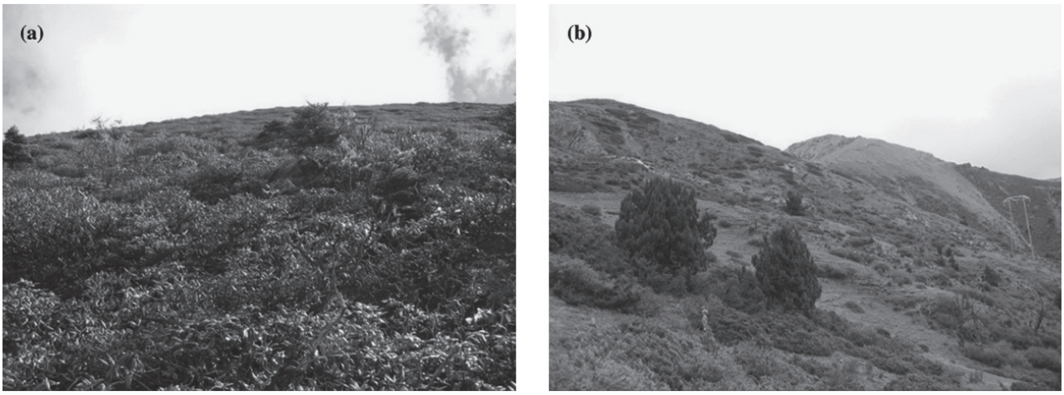


Fig. 1. Spatial structure of *Abies forestii* var. *georgei* (a) on the north-facing slope and *Juniperus saltuaria* (b) on the south-facing slope at treeline in Mountain Baima Xueshan.

maximum stem height, four radii of the vertical crown projection along the two directions marked by the plot axes, and number and type – vertical and stunted, living or dead – of stems in every tree. Heights of all individuals were measured except for those higher than 3 m whose heights were estimated visually. Basal area was calculated including bark.

2.3 Spatial Pattern Analysis

Spatial patterns were analyzed using Ripley's *K* functions (Ripley 1977, 1981), a method that has often been used for point pattern analysis (Moeur 1993). Ripley's *K* function is based on the variance (second-order analysis) of all point-to-point (tree-to-tree) distances in a two-dimensional space (Ripley 1977). The function was defined as:

$$K(t) = \left(\frac{A}{n^2}\right)\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{1}{W_{ij}}I_t(u_{ij}) \quad (i \neq j) \tag{1}$$

Where n is the number of plants in the plot, A is the area of the plot in m^2, u_{ij} is the distance in m between plants i and j. If $u_{ij} \leq t$, $I_t(u_{ij}) = 1$; If $u_{ij} > t$, $I_t(u_{ij}) = 0$. W_{ij} is a circular edge-correction, defined as the inverse of the proportion of a circle of radius, t, placed over each point within the total study area. Monte Carlo simulation (randomly re-positioning all points in the plot and then analyzing the generated plot as before) was used to assess the statistical significance of deviations of $K(t)$ from the null hypothesis of random distribution. This procedure was repeated 99 times and the lowest and highest value of $K(t)$ for each t is used to define the lower and upper bound of a 99% confidence interval. If values of $K(t)$ is positive and exceeds the confidence interval, a clumped distribution can be inferred; if it is negative and exceeds the confidence interval, a regular distribution can be inferred; and if it does not exceed the confidence interval, a random distribution is inferred.

Using $K_{12}(t)$ function, spatial interactions were examined to get information on the spatial relationships between seedlings, saplings and adults. The function was defined as

$$K_{12}(t) = \left(\frac{A}{n_1 n_2}\right)\sum_{i=1}^{n_1}\sum_{j=1}^{n_2}\frac{1}{W_{ij}}I_t(u_{ij}) \tag{2}$$

The function is a generalization of $K(t)$ for a bivariate point process (Diggle 1983, Upton and Fingleton 1985). Monte Carlo simulation was used to assess the statistical significance of deviations of $K_{12}(t)$ from the null hypothesis of spatial independence. Ninety-nine percent confidence interval for $K_{12}(t)$ were generated from 99 toroidal shifts of one size class with respect to the other (Diggle 1983, Upton and Fingleton 1985, Haase 2001). Values of $K_{12}(t)$ exceeding the confidence interval with positive values indicates significant positive association (attraction) between the two tree-classes analyzed; Values of $K_{12}(t)$ exceeding the confidence interval with negative values indicates significant negative association (repulsion); Otherwise, spatial independence.

We calculated $K(t)$ and $K_{12}(t)$ at 2.5 m intervals over the range of distances from 2.5 to 25 m for plots at treeline (1.5 m intervals from 1.5 to 15 m for plots at timberline), where the maximum distance was half the smaller side of the plots. All possible combinations between two types of seedlings, saplings and adults were analyzed in all the four plots. Only those bivariate comparisons that showed significant spatial interaction were presented.

All statistical analysis of the data was performed using the SPPA program (Haase 1995, 2001).

3 Results

3.1 General Characteristics

Population parameters varied between *A. forestii* var. *georgei* and *J. saltuaria*, and for the same species, the parameters were also different from timberline to treeline (Table 1). Among the four stands, *A. forestii* var. *georgei* at timberline had the largest height, mean DBH, basal area and the highest stem density; *J. saltuaria* at treeline showed the lowest values of these parameters except for stem densities of young individuals; even at timberline, the total stem density of *J. saltuaria* was also lower than that of *A. forestii* var. *georgei* at treeline. As for tree size classes, young individuals accounted for a large proportion of *A. forestii* var. *georgei*, with 57.6% and 70.2% seedlings at treeline and timberline, respectively. *J. saltuaria* contained more adults, with 49.4% at treeline and 82.5% at timberline. No seedlings of *J. saltuaria* were found at timberline.

Living stems of *A. forestii* var. *georgei* both at treeline and timberline exhibited reverse *J*- or *L*-shaped distributions, whereas the density of each DBH class at timberline was much higher than that at treeline (Fig. 2a and b). The DBH distribution of *J. saltuaria* at treeline was bell-shaped with its mode 3–6 cm (Fig. 2c), while its DBH distribution at timberline was bimodal and continuous, with two modes in 6–9 cm and 15–18 cm (Fig. 2d).

3.2 Spatial Distribution Pattern of Size Classes

Stem distribution varied between *A. forestii* var. *georgei* and *J. saltuaria*, and for the same species, the distribution patterns were also different from timberline to treeline (Fig. 3). Stems of *A. forestii* var. *georgei* both at treeline and timberline were scattered throughout the plots, and seedlings at timberline tended to be clustered (Fig. 3a and b), while stems of *J. saltuaria* at treeline were mainly distributed in the right part of the plot (Fig. 3c), but its stems at timberline were mostly located in the middle part of the plot (Fig. 3d).

When all size classes of both tree species were analyzed, most of the size classes of *A. forestii* var. *georgei* were significantly ($P<0.01$) clumped but at different distances. Seedlings of *J. saltuaria* at treeline showed random distribution at all distances (Table 2) and saplings of *J. saltuaria* at timberline were randomly distributed at most of the scales. Seedlings and adults of *A. forestii* var. *georgei* at treeline were clumped at all distances up to 25 m, and all of its classes at timberline were also clumped at all distances up to 15 m, while saplings of *A. forestii* var. *georgei* at treeline showed random distribution at scales 4–8 m, 14–15 m and 19–25 m, and clumped at other scales (Table 2). Saplings of *J. saltuaria* at treeline were clustered up to 23 m and randomly distributed between 24–25 m. Adults were randomly distributed within 1–4 m and clustered from 5–25 m. Adults of *J. saltuaria* at timberline showed significant clustering at all distances (Table 2).

3.3 Intraspecific spatial Associations between Different Size Classes

We found different and significant ($P<0.01$) spatial interactions between tree size classes at treeline and timberline of *A. forestii* var. *georgei* and *J. saltuaria* (Fig. 4).The seedlings of *A. forestii* var. *georgei* at treeline showed significant positive correlation to saplings at all scales (Fig. 4a) and to adults up to 21 m distance from each other, while between 22–25 m, seedlings and adults were spatially independent (Fig. 4b); saplings and adults were positively correlated

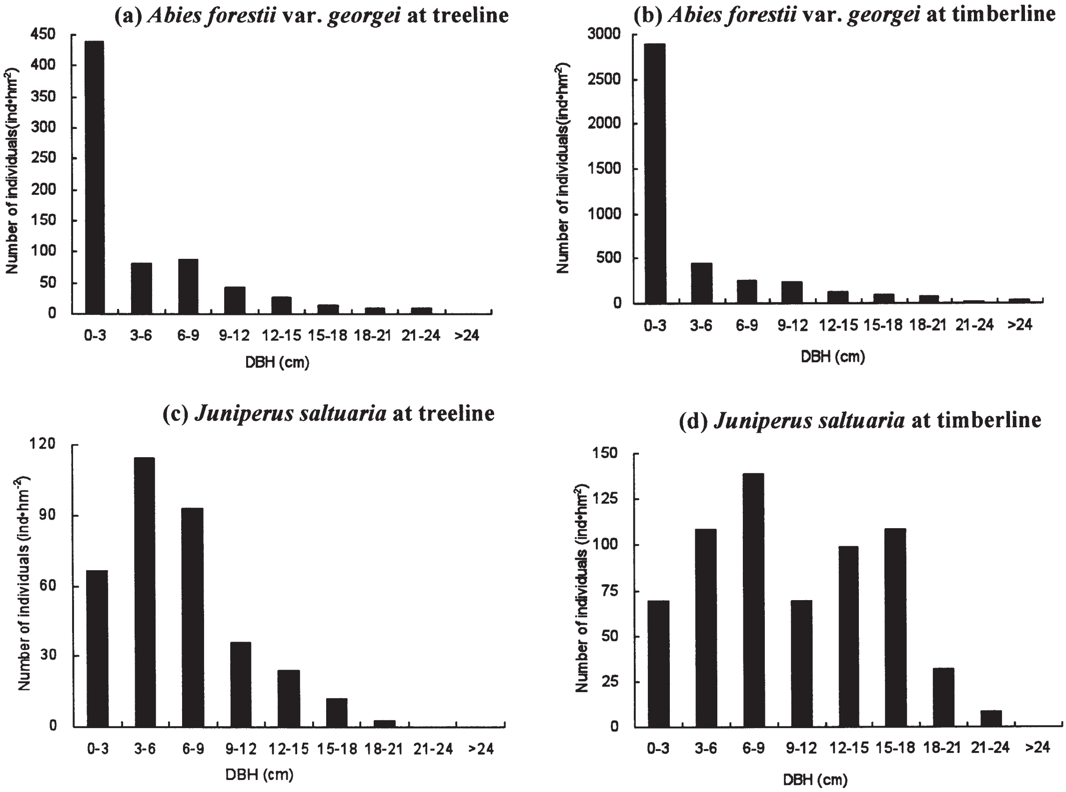


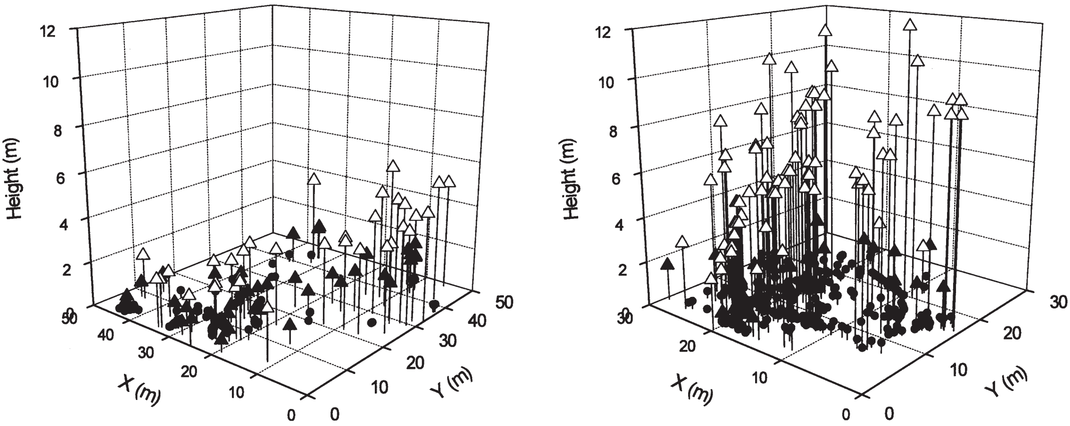
Fig. 2. DBH distributions of *A. forestii* var. *georgei* (a–b) on the north-facing slope and *Juniperus saltuaria* (c–d) on the south-facing slope at treeline and timberline in Mountain Baima Xueshan.

Table 2. Patterns of spatial dispersion for size classes at treeline and timberline of *Abies forestii* var. *georgei* on the north-facing slope and *Juniperus saltuaria* on the south-facing slope in Mountain Baima Xueshan: where the symbols (+) indicate significant (P<0.01) clumped distribution at distance *t* based on *K*(*t*) function values and (•) correspond to a random distribution.

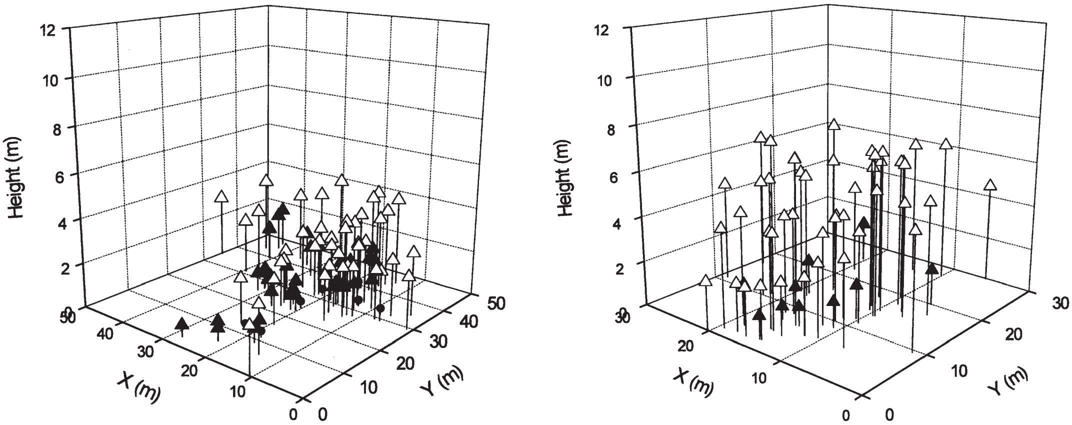
Stand[a]	Classes[b]	n	*t* (m)																								
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
A-Tr	SE	102	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	SA	41	+	+	+	•	•	•	•	•	+	+	+	+	+	•	•	+	+	•	•	•	•	•	•	•	•
	A	34	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
A-Ti	SE	264	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+										
	SA	36	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+										
	A	76	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+										
J-Tr	SE	7	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
	SA	37	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	•	•
	A	43	•	•	•	•	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
J-Ti	SE	0																									
	SA	10	•	•	•	•	+	+	+	+	+	+	•	•	•	•	•										
	A	47	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+										

[a] A-Tr=*Abies forestii* var. *georgei* at treeline, A-Ti=*Abies forestii* var. *georgei* at timberline, J-Tr=*Juniperus saltuaria* at treeline, J-Ti=*J. saltuaria* at timberline;

[b] SE=seedlings, SA=saplings, A=adults.



(a) *Abies forestii* var. *georgei* at treeline **(b)** *Abies forestii* var. *georgei* at timberline



(c) *Juniperus saltuaria* at treeline **(d)** *Juniperus saltuaria* at timberline

Fig. 3. Spatial location and height of all individuals at treeline and timberline for *A. forestii* var. *georgei* on the north-facing slope and *Juniperus saltuaria* on the south-facing slope in Mountain Baima Xueshan. White triangles stand for adults, black triangles stand for saplings, and black dots stand for seedlings.

between 5–17 m (Fig. 4c). The spatial interactions between tree size classes of *A. forestii* var. *georgei* at timberline were significantly positive at almost all the scales (Fig. 4d–f). Positive associations between size classes of *J. saltuaria* on the south-facing slopes were not as significant as that of *A. forestii* var. *georgei*. Only saplings and adults at treeline showed significant positive association at almost all the scales (Fig. 4i). Seedlings at treeline were dominated by spatial independence to adults (Fig. 4h). The seedlings and saplings at treeline showed significant positive correlation at scales ≤22 m and spatial independence between 23–25 m (Fig. 4g); Saplings of *J. saltuaria* at timberline showed different patterns to the adults at different scales: spatial independence at 1–2 m and 12–15 m, slight positive correlation between 3–11 m (Fig. 4j).

4 Discussion

Characteristics of the DBH size class distributions of *A. forestii* var. *georgei* and *J. saltuaria* at treeline and timberline provided important

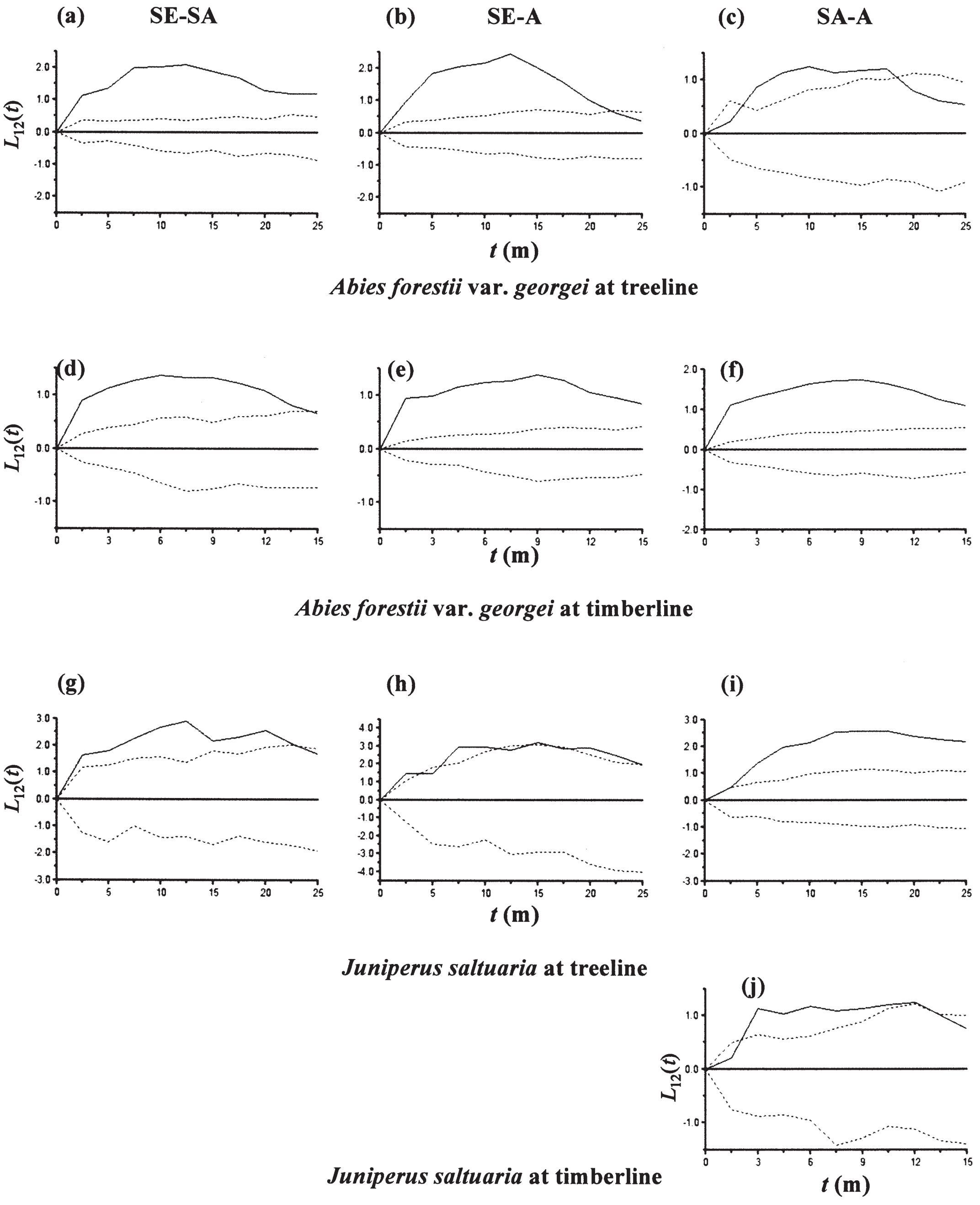


Fig. 4. Intraspecific spatial associations between size classes at treeline and timberline for *A. forestii* var. *georgei* on the north-facing slope and *Juniperus saltuaria* on the south-facing slope in Mountain Baima Xueshan. Black lines indicate observed data ($L_{12}(t)$) from $K_{12}(t)$ function; thin dashed lines indicate the upper and lower 99% confidence intervals through Monte Carlo modeling. Points above the upper interval indicate positive association, points between the intervals indicate no spatial association, and points below the lower interval indicate negative association. Note: SE = seedlings, SA = saplings, A = adults.

information about the regeneration probability of these two species. On the basis of our results, *A. forestii* var. *georgei* were characterized by continuously reverse *J*- or *L*-shaped DBH distributions (living stems) both at treeline and timberline. Similar findings have been reported for other fir species in alpine forests (*A. pinsapo* in southern Spain, *A. mariesii* and *A. veitchii* in central Japan). Sapling or seedling banks of *Abies* are common in the coniferous forest zone, including subalpine and boreal forests (Arista 1995, Kneeshaw et a1. 1998). This may be due to shade tolerance, a characteristic of *Abies* species (Kohyama 1980, Kato and Yamamoto 2000). Seedling density often increases with decreasing altitude (e.g., Wardle 1971, Young 1993, Šrůtek and Lepš 1994, Arévalo and Fernández-Palacios 2003). Our results showed the similar trend in *A. forestii* var. *georgei* seedling and sapling density from treeline to timberline, and significant negative correlation can be found between shrub cover and number of seedlings (Table 1). The reason may be that seedling establishment was greater in gaps than under closed canopy (Liu 2004). A similar response has been found in other *Abies* spp. (Arista 1995, Wilson 199l). Higher occurrence of seedlings in the gaps can be attributed to several factors, including more intense seed rain, better germination capacity and higher survivorship of seedlings in gap areas (Arista 1995, Liu 2004). The huge number of seedlings of *A. forestii* var. *georgei* especially at timberline is consistent with previous ideas based on the "seedling bank" concept because rapid germination of these limited treeline populations could decrease seed mortality and produce a seedling bank as an establishment source instead of a seed bank (Payette et a1. 1982, Camarero et a1. 2000).

However, *J. saltuaria* exhibited very different regeneration characteristics from *A. forestii* var. *georgei*. There were much less seedlings of *J. saltuaria* on the south-facing slope than *A. forestii* var. *georgei* on the north-facing slope at treeline, and no seedlings of *J. saltuaria* were found at timberline. *Junipers* are especially well adapted to the south-facing slope's high insolation and extreme diurnal ranges of temperature (Winkler 2000, Miehe et al. 2006, 2008). In mature forests, natural regeneration of *Juniperus* was usually satisfactory with numerous young seedlings under the sparse canopy of the forest (4000 to 5000 per ha), and it shared the same mortality rate as *Abies* spp. on north-facing slopes of about 90% (Li 1993, Zhang 2007). Mountain pastoralism (which will be discussed in the following part) on the south-facing slopes may play an important role in the disappearance of *Juniperus* seedlings. Though the seedlings themselves are usually not browsed due to the foliage's high aromatic oil content (Ku and Cheo 1941), they were damaged through animal trampling. Consistent with this, more seedlings were found inside shrubs protected from trampling at treeline.

Size classes of *A. forestii* var. *georgei* were mainly clustered. Similar results were found for size classes in the subalpine forest-alpine grassland ecotones of the Spanish Central Pyrenees (Camarero et a1. 2000). It seemed that clumps of trees could create more favorable microenvironments than those available for isolated trees (Tranquillini 1979). Facilitated by the microsites of tree islands, seedlings showed highest clumping intensity and scale. The clumped distribution of adults at all distances could indicate their possible origin near their parents (Lavoie and Payette 1992). The trend towards random distribution for saplings of *A. forestii* var. *georgei* at treeline suggested a more marked competition for space and resources (e.g., light and soil nutrients) with the dense shrubs, most of which had the same height as the saplings.

All size classes of *A. forestii* var. *georgei* on the north-facing slopes showed positive associations with each other. Positive plant interactions have been studied in harsh environments like arctic tundra and alpine communities (Carlsson and Callaghan 1991, Bertness and Callaway 1994, Kikvidze and Nakhutsrishvili 1998, Šrůtek et a1. 2002). Studies also found that intraspecific positive interactions can buffer seedlings from extreme conditions at treeline (Kullman 1983, Payette and Filion 1985, Taylor 1995). These results suggested that stressful environments may lead to facilitating relationships.

Stems of *J. saltuaria* at treeline and timberline were found mainly distributed where growing with dense shrubs (Fig. 1b). Mountain pastoralism might be the main factor controlling these distribution patterns on the south-facing slope. Vertical agropastoral transhumance [a traditional livelihood strategy for people inhabiting mountainous regions, who complementarily exploit resources at different elevations through a combination of pastoral management and crop cultivation (Uhlig 1995, Yi et al. 2007)] is one of the main livelihood strategies for the local Tibetans. They depend on a combination of activities at different elevations for a basic livelihood, relying heavily on forest resources and livestock. Grazing, deforestation, burning slopes and herb-collecting were the main human impacts in this area. In Mountain Baima Xueshan, the vertical change of climate caused by the variation of topography leads to the formation of different seasonal pastures, and the seasonal difference of grazing time, i.e. seasonal pastoralism (Winkler 1998). Generally, there was no grazing in the north-facing slope because of long lasting snow cover. The alpine area pastures in the south-facing slope are usually used as the ideal pastures in summer because of the cool, rainy weather, and the abundant grasses there (Wu and Liu 1998). There are at least 4000–4500 yaks in the natural reserve and most of them grazed seasonally on the south-facing slopes (Bao and Wu 1998), which degraded the south-facing slopes. Under the protection of procumbent *J. squamata*, stems survived without trampling of herds. Photographs also showed more stems inside the dense *J. squamata*. As for tree size classes, the random distribution of seedlings at treeline and saplings at timberline of *J. saltuaria* may be related to the small number of seedlings that survived trampling by herds.

Our results clearly showed that spatial structure varied between *A. forestii* var. *georgei* on the north-facing slopes and *J. saltuaria* on the south-facing slopes, and for the same species, the spatial structure were also different from timberline to treeline. Stem density, mean tree height and number of young individuals of *A. forestii* var. *georgei* were significantly higher than those of *J. saltuaria*. For the same species, they were different from timberline to treeline, *i.e.*, stem density and mean tree height of both species became lower with increasing elevation. Trees of both species were mainly clustered either at treeline or at timberline, but spatial patterns of young *J. saltuaria* were mainly dominated by random patterns. When intraspecific spatial associations were analyzed, most of the tree size classes showed positive associations, but positive associations between size classes of *J. saltuaria* on the south-facing slopes were not as significant as that of *A. forestii* var. *georgei*. Based on a single sample plot per species per elevation, the results may not be generalized over the whole region, but the findings can improve our knowledge about the general characteristics and spatial patterns of treeline species in the Mountain Baima Xueshan. However, there are still many questions lacking definitive answers, *i.e.*, treeline dynamics following global warming and mechanistic explanations for the retreat of treeline on south-facing slopes. So, we recognize the necessity of long-term studies of permanent plots for monitoring the long-term effects of livestock herding and climate change in this area.

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References

Arévalo, J.R. & Fernández-Palacios, J.M. 2003. Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands. Plant Ecology 165: 1–10.

Arista, M. 1995. The structure and dynamics of an Abies pinsapo forest in southern Spain. Forest Ecology and Management 74: 81–89.

Bao, W.K. & Wu, N. 2003. Human-induced disturbance on alpine and subalpine meadow and its aftereffects in Deqin County of the northwestern Yunnan province. Grassland of China 25(2): 1–8.

Bertness, M.D. & Callaway, R. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191–193.

Camarero, J.J., Gutiérrez, E. & Fortin, M.J. 2000.

Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. Forest Ecology and Management 134(1–3): 1–16.

Carlsson, B.A. & Callaghan, T.V. 1991. Positive plant interactions in tundra vegetation and the importance of shelter. Journal of Ecology 79: 973–983.

Chen, J. & Bradshaw, G.A. 1999. Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. Forest Ecology and Management 120(1–3): 219–233.

Diggle, P.J. 1983. Statistical analysis of spatial point patterns. Academic Press, London. 148 p.

Duncan, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecology 79: 1073–1084.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. Journal of Vegetation Science 6: 575–582.

— 2001. Can isotropy vs. anisotropy in the spatial association of plant species resolve physical vs. biotic facilitation? Journal of Vegetation Science 12: 127–134.

Hao, Z.Q., Zhang, J., Song, B., Ye, J. & Li, B.H. 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. Forest Ecology and Management 252(1–3): 1–11.

Kato, K. & Yamamoto, S. 2000. Effects of canopy on the sapling composition and structure in a subalpine old-growth forest, central Japan. Ecoscience 7: 237–242.

Kikvidze, Z. & Nakhutsrishvili, G. 1998. Facilitation in subnival vegetation patches. Journal of Vegetation Science 9: 261–264.

Kneeshaw, D.D. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79(3): 783–794.

Kohyama, T. 1980. Growth pattern of Abies mariesii saplings under conditions of open-growth and suppression. Botanical Magazine (Tokyo) 93: 13–24.

Ku, C.C. & Cheo, Y.C. 1941. A preliminary survey of the forests in W-China. Sinensia 12: 81–113.

Kullman, L. 1983. Short-term population trends of isolated treelimit stands of Pinus sylvestris L. in central Sweden. Arctic and Alpine Research 15:369–382.

Lavoie, C. & Payette, S. 1992. Black spruce growth forms as a record of a changing winter environment at treeline, Quebec, Canada. Arctic and Alpine Research 24: 40–49.

Li, W.H. 1993. Forests of the Himalayan Hengduan Mountains of China and a strategy for their sustainable development. ICIMOD, Kathmandu. 175 p.

Liu, Q. 2002. Ecological research on subalpine coniferous forests in China. Sichuan University Press, Chengdu.

— 2004. The effects of gap size and within gap position on the survival and growth of natural regenerated Abies georgei seedlings. Acta Phytoecologica Sinica 28(2): 204–209.

Miehe, G., Miehe, S., Schlütz, F., Kaiser K. & La, D. 2006. Palaeoecological and experimental evidence of former forests and woodlands in the treeless desert pastures of Southern Tibet (Lhasa, A.R. Xizang, China). Palaeogeography, Palaeoclimatology, Palaeoecology 242: 54–67.

— Miehe, S., Will, M., Opgenoorth, L., La, D., Tsering, D. & Liu, J.Q. 2008. An inventory of forest relicts in the pastures of Southern Tibet (Xizang A.R., China). Plant Ecology 194: 157–177.

Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. Forest Science 39: 756–775.

Payette, S., Deshaye, J. & Gilbert, H. 1982. Tree seed populations at the treeline in Rivière aux Feuilles area, northern Quebec, Canada. Arctic and Alpine Research 14: 215–221.

— & Filion, L. 1985. White spruce expansion at the tree line and recent climatic change. Canadian Journal of Forest Research 15: 241–251.

Ripley, B.D. 1977. Modeling spatial patterns. Journal of the Royal Statistical Society, B39: 172–212.

— 1981. Spatial statistics. Wiley, New York.

Schickhoff, U. 2006. The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. In: Broll, G., Keplin B. (eds.). Mountain ecosystems: studies in treeline ecology. Springer-Verlag Berlin Heidelberg. p. 275–354.

Schurr, F.M., Bossdorf, O., Milton, S.J. & Schumacher, J. 2004. Spatial pattern formation in semi-arid shrubland: a priori predicted versus observed pattern characteristics. Plant Ecology 173(2): 271–282.

Šrůtek, M., Doležal, J. & Hara, T. 2002. Spatial structure and associations in a Pinus canariensis population at the treeline, Pico del Teide, Tenerife, Canary Islands. Arctic and Alpine Research 34(2):

201–210.

— & Lepš, J. 1994. Variation in structure of Larix olgensis stand along altitudinal gradient on Paektusan, Changbaishan, North Korea. Arctic and Alpine Research 26: 166–173.

Sun, H.L. & Zheng, D. 1998. Formation, evolution and development of Qinghai-Tibetan Plateau. Guangdong Science and Technology Press, Guangzhou.

Taylor, A.H. 1995. Forest expansion and climate change in the Mountain Hemlock (Tsuga mertensiana) Zone, Lassen National Park, California, USA. Arctic and Alpine Research 27: 207–216.

Tomppo, E. 1986. Models and methods for analyzing spatial patterns of trees. Communicationes Instituti Forestalis Fenniae 138.

Tranquillini, W. 1979. Physiological ecology of alpine timberline. Springer Verlag, New York. 137 p.

Uhlig, H. 1995. Persistence and change in high mountain agricultural systems. Mountain Research and Development 15(3): 199–213.

Upton, G.J. & Fingleton, B. 1985. Spatial data analysis by example. Vol. 1. Point pattern and quantitative data. Wiley, New York.

Wang, T., Liang, Y., Ren, H.B., Yu, D., Ni, J. & Ma, K.P. 2004. Age structure of Picea schrenkiana forest along an altitudinal gradient in the central Tianshan Mountains, northwestern China. Forest Ecology and Management 196(2–3): 267–274.

Wardle, P. 1971. An explanation for alpine timberline. New Zealand Journal of Botany 9: 371–402.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1–22.

Wiegand, K., Jeltsch, F. & Ward, D. 2000. Do spatial effects play a role in the spatial distribution of desert-dwelling Acacia raddiana? Journal of Vegetation Science 11 (4): 473–484.

Wilson, M.V. 1991. Age structure patterns in Abies amabilis stands of the Cascade Mountains. American Midland Naturalist 125: 331–339.

Winkler, D. 1998. The forests of the eastern part of the Tibetan Plateau – a case study from Jiuzhaigou (Zitsa Degu; NNW Sichuan). Plant Research and Development 47/48.

— 2000. Patterns of forest distribution and the impact of fire and pastoralism in the forest region of the Tibetan Plateau. In: Miehe, G., Zhang Y.L. (eds.). Environmental change in High Asia. Marburger Geographische Schriften 135: 201–227.

Wu, N. & Liu, Z.G. 1998. Probing into the causes of geographical pattern of subalpine vegetation in eastern Qinghai-Tibetan Plateau. Chinese Journal of Applied and Environmental Biology 4(3): 290–297.

Yi, S.L., Wu, N., Luo, P., Wang, Q., Shi, F.S., Sun, G. & Ma, J.Z. 2007. Changes in livestock migration patterns in a Tibetan-style agropastoral system – a study in the Three-Parallel-Rivers region of Yunnan, China. Mountain Research and Development 27(2): 138–145.

Young, K.R. 1993. Tropical timberlines: changes in forest structure and regeneration between two Peruvian timberline margins. Arctic and Alpine Research 25: 167–174.

Zhang, Q.Y., Zhang, Y.C., Luo, P., Wang, Q. & Wu, N. 2007. Ecological characteristics of a Juniperus saltuaria population at timberline on the south-facing slope of Mountain Baima Xueshan, Southwest China. Journal of Plant Ecology 31(5): 857–864.

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