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林窗对长苞冷杉自然更新幼苗存活和生长的影响

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摘 要 长苞冷杉（*Abies georgei*）林是我国西南亚高山针叶林的重要类型之一，分布于海拔 3 200～4 200 m。目前对于该森林林窗对树苗更新的调节还很少了解。通过 1997～2000 年对 20 个林窗的连续观测调查，研究了滇西北白马雪山自然保护区西坡亚高山长苞冷杉林林窗大小和林窗位置对自然更新幼苗存活和生长的影响。长苞冷杉针叶林林窗大小分布为，面积大于 100 m^2 的大林窗占 20%左右，中等林窗面积为 50～100 m^2，占 35%左右，小林窗面积小于 50 m^2，占 45%左右。4 个生长季节的连续观测结果表明 林窗与林下非林窗内的幼苗大小和幼苗存活数量差异明显。林窗由小到大，单位面积内的自然更新苗木数量逐渐增加，大林窗中更新苗为小林窗的 1.5 倍左右，而林下的更新苗很少，0.5 ind.·10 m^{-2}。中等林窗和小林窗内的幼苗数量在从南到中心到北的位置上几乎没有明显的差异 大林窗中存在由南到北的位置差异，更新幼苗数量逐渐增加。从更新幼苗的生长来看，中等林窗内的幼苗，高度最大、生长最快，定居阶段的平均年高生长为（7.8±0.5） cm·a^{-1}，小林窗次之，大林窗和林下幼苗个体最小，生长最慢。更新幼苗的基径随林窗大小的变化与高度变化相似。进一步从林窗位置来看，中、小林窗幼苗大小和年平均高生长量几乎无位置差异，大林窗则由南到北，幼苗由大变小，年高生长量逐渐减低。从幼苗存活数量、生长大小来看，中等林窗大小是长苞冷杉幼苗更新的适宜面积，这为该类型退化亚高山针叶林恢复提供了一定的参考。

关键词 长苞冷杉 林窗 自然更新 幼苗 存活 生长 亚高山针叶林

THE EFFECTS OF GAP SIZE AND WITHIN GAP POSITION ON THE SURVIVAL AND GROWTH OF NATURALLY REGENERATED *ABIES GEORGEI* SEEDLINGS

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Abstract The survival and growth of *Abies georgei* seedlings growing in forest canopy gaps was investigated over a 4-year period on the Baima Snow Mountain in northwest Yunnan Province，China. Of the total gaps surveyed in *A*. *georgei* forests，45% were small (gap area < 50 m^2)，35% were medium sized (50–100 m^2) and 20% were large (> 100 m^2) gaps. Seedling growth rates，survivorship，abundance and size were measured and compared among the three different sized gaps and under the closed forest canopy and within gaps according to their position (north，south and center) in each gap. The seedlings all originated from natural seed rain. The results showed that there were significant differences in the size and number of seedlings among the different sized gaps and understorey. There were 1.5 times more seedlings in larger gaps than in smaller ones and very few seedlings (0.5 ind.·10 m^{-2}) were found in the understory. The survival of *A*. *georgei* seedlings within gaps tended to increase from south to north positions within the larger gaps，whereas survivorship did not vary within the small and medium sized gaps. Seedling size，in terms of both height and basal diameter，in the different sized gaps was as follows：medium > small > large > understorey. Relative growth rates showed a similar pattern. The average annual growth in height was (7.8±0.5) cm in medium gaps. Furthermore，size and annual relative height growth of seedlings did not differ significantly among positions within the medium and small gaps，but seedling height peaked in the southern position of large gaps and de-

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clined towards the center and north edges. Seedling establishment was greater in gaps than under the closed-canopy. Due to adaptation to light conditions, relative growth rates of seedlings were greatest in medium sized gaps but were relatively low in regions of the large gaps that had greater exposure to direct solar radiation as well as in small gaps that were shaded and received little direct solar radiation. Finally, based on observed changes in survival and growth of seedlings over four growing seasons, the author suggests that medium sized forest canopy gaps provide the best habitat for regeneration of *A. georgei* seedlings.
Key words *Abies georgei*, Forest gap, Natural regeneration, Seedling, Survival, Growth, Subalpine coniferous forest

Abies georgei forest is one of the major subalpine coniferous forests in the southwest of China, and distribute on subalpine range from 3 200 to 4 200 m above sea level (Liu *et al*., 2001a). The subalpine coniferous forest has important ecological roles such as conserving water and soil, and biological diversity, and is accredited as the significant ecological barrier of the regions in eastern edges of Tibet Plateau and the upper reaches of the Yangtze River (Liu *et al*., 2001b; Liu, 2002). Unfortunately, the forest has been severely destroyed and few of primitive vegetation are preserved in the past decades years. At present, most of the subalpine coniferous forests in southwestern China are in different states of degradation. Thus, it is very urgent to restore the damaged these forest ecosystems.

Forest gaps created by the death of one or more trees are critical in the community dynamics of many forest types (Pickett & White, 1985). It is very important for natural regeneration (e.g. establishment and growth of different tree species) of forests (Canham, 1990; Cintra & Horna, 1997). Nevertheless, the role of canopy gaps in forest development is only partially understood. The role has been documented both in temperate forests and in tropical forests (Brokaw, 1985; Poulson & Platt, 1989; Runkle, 1982; Zang, 1998), but has paid much less attention to coniferous forests, especially to subalpine coniferous forest (Kenneth, 1992; Li, 1990; Xia *et al*., 1996).

The invasion of shade-tolerant species to gaps appears to be associated with gaps created (Gray & Spies, 1996), but it is not clear whether it is a response to gap size or to micro-environments within canopy gaps created by mortality of dominant trees. Thus it is important to know how canopy gaps influence early phase of the natural regeneration of old-growth coniferous subalpine forests. Establishment and growth of forest trees should be correlated with gap size and within-gap position and such patterns are seen in many forests (Poulson & Platt, 1989; Runkle, 1982; Gray & Spies, 1996; Brandani *et al*., 1988).

The controls on tree seedling establishment in relation to canopy gaps within subalpine coniferous forests in southwestern China are poorly understood. Therefore, the purpose of this paper is to 1) determine whether the establishment and growth of the *Abies georgei* seedlings are affected by gap size and within-gap position, i.e., what fate of the naturally regenerated seedlings in different sized gaps, and 2) whether the survival of *Abies georgei* seedling was better in gap than non-gaps (understorey). The survey described in this paper is part of a larger study; future papers will demonstrate the effects of seed germination in forest canopy gaps.

1 Materials and Methods

1.1 Study site

The study was conducted at the west slope of Baima Snow Mountain Natural Reserve (27°47′–28°36′ N, 98°57′–99°21′ E, 3 800–4 000 m above sea level) in northwestern Yunnan, China. The observation reported here was made between September 1997 and October 2000. Annual rainfall at study site is 650.5 mm, annual evaporation is 566.1 mm and relative humidity is 82%. Annual mean temperature is 4.7 ℃, the extreme minimum temperature is –18.6 ℃ in January and extreme maximum temperature is 15.8 ℃ in August (Yunnan Province Academy of Forestry Planning, 1989). The content of soil organic matter of the subalpine coniferous forest is 2.82%–3.65%, and soil pH is 5.6–5.9.

Subalpine coniferous forests form the natural vegetation of this zone and still cover considerable parts of the site. The vegetation belt (from 3 500 to 4 200 m asl. wide) is dominated by *Abies georgei* in tree layer, *Rhododendron* sp. in shrub layer and moss on the ground layer (Liu *et al*., 2001a). *A. georgei* is able to regenerate naturally in the study site.

1.2 Species

Abies georgei is one of the major evergreen coniferous tree species in subalpine zone in the southwest of China. *A. georgei* forest is natural and often mixed with other species of *Abies* and *Picea* in tree layer in the study area, and tree density averages 320–460 adult trees per hectare. Height of the canopy often was 8–18 m, sometimes up to 25 m, and diameter at breast height (*DBH*) ranges from 12 to 36 cm.

1.3 Experimental design

Twenty gaps were measured with diameter (lengths of the major and minor axes measured between tree crown edges) in the study area, and selected 15 different sized gaps for the seedlings experiment in September 1997. These gaps were created by the death of one or more trees or from disturbance due to human activity in the study site in terms of cutting and so on. Understorey vegetation is almost the same in the gaps.

This study was designed to follow the fate of seedlings originating from natural seed rain in different sized natural gaps. Three sizes of these gaps, with two replicates of each gap size, were chosen in the *Abies georgei* forest stands. Measured and chosen gaps size was divided into three scales: small (<50 m^2), medium (50 – 100 m^2) and large (>100 m^2). All chosen forest gaps were located in areas with slopes less than 20% and with relatively identified understorey in each. Three understorey sites equal in area to the large gap size, were randomly established in the stand. Each gap was subdivided into a lot of 6-m^2 plots. Three within-gap positions (north, south and center) were identified in each gap (Fig. 1).

In late spring or early summer of 1997, many of the seedlings emerged in the gaps. The individuals of first-year *Abies georgei* within plots in different sized gaps and control plots was searched and marked with red paint on the basal shoots.

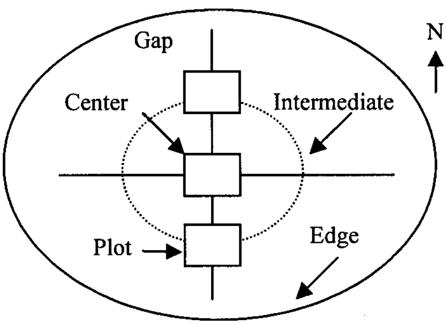

Fig. 1 The plots in canopy gap of subalpine *Abies georgei* forest

1.4 Measurements

Height and basal diameter of first-year seedlings among different sized gaps and control plots were not significantly different according to Tukey's honestly significant difference (Proc One-way ANOVA, SAS Inc., 1988), i.e., (2.6 ± 0.2) cm of height and (0.3 ± 0.04) cm of basal diameter (mean ± SE). Marked seedlings were revisited in September 1998, 1999 and 2000. Size (i.e. basal diameter and height) of naturally regenerated seedlings of *Abies georgei* from the 1997 cohort within 2 m × 3 m of each plot was measured in different sized gaps and the control. Seedlings were considered dead when they were missing, cut at the stem, or entirely lacking green color. At the same time, seedlings were counted in each plot. Seedlings were considered "established" if they were alive at the end of the experiment.

1.5 Data analysis

Due to the very low number of naturally regenerated *Abies georgei* seedlings in the study site, all seedlings from different position in each gap were regarded as overall to calculate for natural regeneration analysis. The effects of gap size and within-gap position on seedling survival, seedling size (height and basal diameter) and relative height growth (*RHG*, (final height – initial height)/3 years) were determined with one-way analysis of variance (ANOVA) for among four treatments: control, small, medium and large. Results with a probability higher than $p > 0.05$ were considered as not statistically significant. All analyses were conducted using SPSS 11.5 for Windows (SPSS Inc., Chicago, USA).

2 Results

2.1 Gap characteristics

Most gaps had an elliptical shape, and gap area was calculated using the formula for an ellipse. $A = 2\pi LW/4$, which L and W are the lengths of the major and minor axes. The mean gap area was 82 m^2 (range 16 – 230 m^2; $n = 20$). Canopy gaps were divided into large (>100 m^2), medium (50 – 100 m^2) and small (<50 m^2) gaps, in which there are 45% of small, 35% of middle and 20% of large gaps in *Abies georgei* forest (Fig. 2).

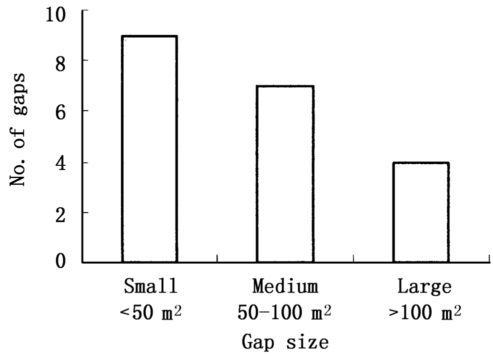

Fig. 2 Distribution of gap size at Baima Snow Mountain, Yunnan, China
A total of 20 gaps, in which small (<50 m^2) 9, medium (50 – 100 m^2) 7 and large (>100 m^2) 4

2.2 Seedling survival

At the end of the experiment (2000), the difference of survival number of naturally seeded *Abies georgei* seedlings varied significantly between control (understorey) and canopy gaps ($F = 9.37$, $p < 0.05$). At the beginning of the experiment (1997), *Abies georgei* seedling density was great in the understorey, whereas the seedling density was small in all gaps, i.e. average 28 individuals in control and 13 individuals in whole gaps per 10 m^2, respectively. There were more 1-year and 2-year old *Abies georgei* seedlings in understorey sites than in the gaps.

However, survival of naturally regenerated seedlings after four growing seasons in gaps is more than in the control, i.e. 0.5 individuals in control and 1.2 individuals per 10 m^2 in whole gaps, respectively. The seedlings survival was significantly lower in small and medium gaps (small ≈ medium) than in large gaps, and the lowest in control at the end of the experiment. The number of the seedling survival in large gaps was 200% greater than in control, 100% and 133% higher in small and medium gaps.

ANOVA analysis indicated that survival of the seedlings after four growing seasons differed significantly by gap size (Table 1). The survival of *Abies georgei* seedlings increased with gap size, for example, this change of survival of the seedlings within northern position was showed in Fig. 3. Average survival of the seedlings was approximately 1.5 times in large gaps than small ones at the end of the experiment. In addition, the survival of the seedlings in different within-gap position was also significantly different by different sized gaps (Table 1).

After four growing seasons (this survival seedlings were also called "establishment" ones), survival of *Abies georgei* seedlings were significantly different and tended to increase from southern through central to northern positions within large gaps ($F = 5.68$, $p < 0.05$), whereas differences of survival of the seedlings were not significant at different gap positions in small and medium gaps, respectively ($F = 1.97$, $p > 0.05$ and $F = 3.29$, $p > 0.05$) (Fig.4).

Table 1　ANOVA table for significance test the effects of gap size and within-gap position on survival, height, *RHG* of *Abies georgei* seedlings after four growing seasons

	Source	Sum of squares	*df*	Mean square	*F*	Significance
Survival	Within-gap position	0.244	2	0.122	8.082	0.002
	Gap size	0.587	13	0.045	2.991	0.007
Height	Within-gap position	18.742	2	9. 371	14.053	0.000
	Gap size	449.394	13	34.569	51.840	0.000
RHG	Within-gap position	0.770	2	0.385	22.287	0.000
	Gap size	98.426	13	7.571	438.405	0.000

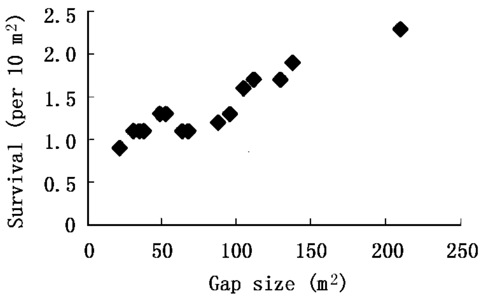

Fig.3　Survival of *Abies georgei* seedlings after four growing seasons by gap size (within northern position)

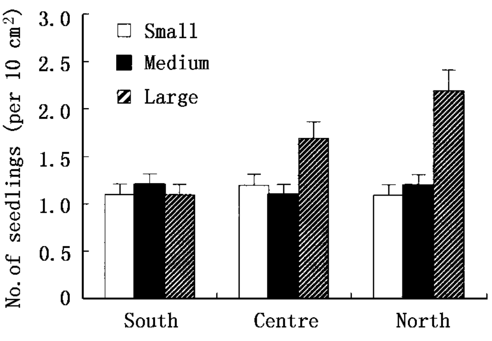

Fig.4　Survival of natural regeneration after four growing seasons by positions within-gaps
Bars indicate mean ± SE ($n = 5$)

2.3　Seedling growth

Compared with control, gap size had a significant effect on the size of naturally regenerated *Abies georgei* seedlings in terms of the height, basal diameter and *RHG* (mean annual height growth) of the seedling after four growing seasons ($F = 5.11$, $p < 0.05$, $F = 3.84$, $p < 0.05$ and $F = 4.27$, $p < 0.05$, respectively).

The effects of gap size and within-gap position on height and *RHG* of *Abies georgei* seedlings were significantly different (Table 1). The size of naturally regenerated seedlings in different sized gaps varied greatly. For example, distribution of height of *Abies georgei* seedlings in different sized gaps (within northern position) was showed in Fig.5. The largest individuals both in height and basal diameter occurred in medium gaps, immediate individuals in small gaps, the third in size in large gaps and the smallest individuals in control. The average annual *RHG* changes was medium > small > large > control. The average annual *RHG* of seedlings in medium gaps was approximate two times of the large gaps, three times of control sites (Table 2).

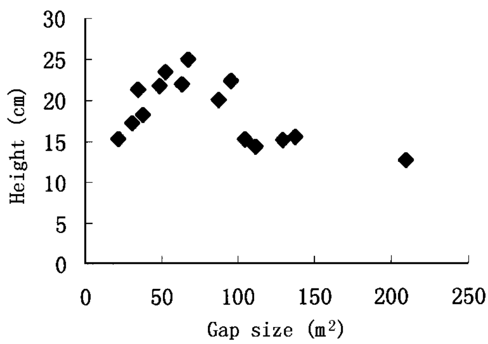

Fig.5　Height of naturally regenerated *Abies georgei* seedlings after four growing seasons in different sized gaps (within northern position)

Table 2 Effects of gap size on growth of *Abies georgei* seedlings after four years of regeneration (numbers are mean ± SE, $n = 5$)

Measurement	Small	Medium	Large	Control
Height (cm)	17 ± 1.4	24.5 ± 2.7	14.8 ± 1.9	9.9 ± 1.2
Basal diameter (cm)	2.5 ± 0.3	2.9 ± 0.3	2.0 ± 0.2	1.7 ± 0.2
RHG ($cm \cdot a^{-1}$)	4.7 ± 0.2	7.8 ± 0.5	4.2 ± 0.4	2.4 ± 0.1

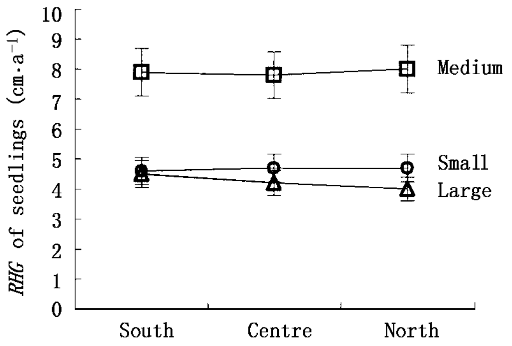

Fig.6 The average annual relative height growth (*RHG*) of naturally regenerated *Abies georgei* seedlings after four growing seasons on the north-south transects in different sized gaps

RHG is (final height − initial height)/3 years. Bars indicate mean ± SE ($n = 5$)

Furthermore, if fifteen gaps were divided into three types of sized gaps (small, medium and large, the same above), the results were found that the average annual *RHG* of naturally regenerated *Abies georgei* seedlings was significantly different within-gap positions in large gaps ($F = 7.27$, $p < 0.05$), and were no significantly different in medium and small gaps ($F = 0.86$, $p > 0.05$ and $F = 2.23$, $p > 0.05$, respectively) at the end of the experiment. The *RHG* of the seedlings along the north-south transects of the large gaps, declined from the southern parts towards the central and northern parts (Fig. 6).

3 Discussion

Although natural regeneration of subalpine coniferous forests in western China was often reported in the past decade (Li, 1990; Wang & Xu, 1995; Wu, 1999; Sichuan Forests Editorial Committee, 1992; Liu & Wu, 2002), this is the first study that examined the process of seedling establishment for *Abies georgei* over a range of gap size.

The seedlings of *Abies georgei* is considered being shade-tolerant (Chinese Forests Editorial Committee, 1999), however, the seedlings in understorey had lower survival rate than that in gaps. High mortality of *Abies georgei* seedlings in closed-canopy forest in the study occurred during the first and second growing season after emergence. Meanwhile, it is valuable attention that there were a lot of younger *Abies georgei* seedlings in understorey sites than in the gaps at the early period. It is likely that suitable light levels in the understorey helpful for the seed germination (Chinese Forests Editorial Committee, 1999).

This study showed that greater seedling density occurred in gaps. Establishment of *Abies georgei* seedlings varied significantly among different sized gaps, but no significantly among within-gap positions in medium and small gaps, while establishment of the seedlings tended to be higher in southern positions of large gaps and establishment of the seedlings was the lowest in control areas. The result is not similar to that of Gray 's study on gap size effects in Douglas-fir forests (Gray & Spies, 1996). The causes must be studied further in the future. In a word, it is during the seedling establishing stages when most mortality occurs. High mortality at early stages limits the number of recruits a plant population can produce.

Seedling growth response appeared to differ among different sized gaps. Growth rate with gap size are medium > small > large > control. In addition, average annual relative height growth of the seedlings also is varied in different positions in large gaps, that is particularly gradually increase from northern through central to southern positions of gaps, possibly due to suitable light levels and the undense shrub and herb layers in the southern parts of the gaps.

Why was the seedling growth rate greater in medium gap and southern positions of large gaps than those in other gaps and positions? The younger *Abies georgei* seedlings are shade-tolerant and are adapted to grow in shade condition that is approximate 20% light levels (Liu, 2002). The environmental conditions (e.g. light, temperature) are different in different sized gaps and within gap positions (Liu *et al.*, 2000; Wang *et al.*, 2000; Zhang *et al.*, 2001). The seedlings in large gaps were more exposed to direct solar radiation and those in medium and small gaps were shaded to weak solar radiation, and the seedlings of north position in large gaps also were more exposed to direct solar radiation than those of south position (because trees in surrounding gap block off from south solar radiation). The southern edges of large gaps were the only zones that received indirect solar radiation and are shade in this study (Liu & Wu, 2002). So growth rate of the seedlings in southern positions was higher than in central and nothern positions in large gaps because of its shade-tolerant trait.

Locations with the greatest survival often had relatively low growth, and vice-versa. This is just the same to that of Gray and Spies (1996) in conifer seedling when working with gap size and position treatments. In understorey, low resource levels (e.g. light) may have limited survival as well as growth. The seedlings at south positions were taller but with lower density, smaller but with higher density at north positions in large gaps. Hence, moderate resource levels in shaded gaps may have been sufficient to ensure high growth rates, but not survival. High light levels in exposed gap locations may have led to low growth rates of established seedlings.

This study suggests that gap size and within-gap position are also important determinants for regeneration of *Abies georgei* forest, canopy gaps in subalpine coniferous forests are important sites for establishment of conifer seedlings, and that medium gap size is favourable area for regeneration of *Abies georgei* forest based on the changes of survival and growth of seedlings for four growing years in the early period. *Abies georgei* seedling growth rates in this study were quite low in large gaps and understorey, although relative high survival rates. The medium gaps may be important sites for forest development by allowing abundant establishment and relatively high growth rates of established seedlings because of the greatest *RHG* and size.

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