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RESEARCH ARTICLE

Effects of gap microsites and bamboo on *Abies faxoniana* regeneration in a subalpine forest, China

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To clarify the effects of gap size and age, as well as microsites on *Abies faxoniana* recruitment in gaps with or without dwarf bamboo, the occurrences of *A. faxoniana* seedlings and saplings on four microsites were examined in a subalpine forest in Wanglang Natural Reserve, southwestern China. Results showed that: (1) while increased gap size had little effect on the seedling densities, it significantly reduced the sapling densities on moss-cover ground in A gaps (without bamboos) and those on moss-cover ground and decaying logs in AF gaps (with bamboos; $P < 0.05$). (2) Increased gap age also exerted little effect on the seedling densities while significantly reduced the sapling densities on decaying logs in AF gaps ($P < 0.05$). (3) Most of *A. faxoniana* seedlings and saplings occurred on decaying logs in AF gaps, but in A gaps *A. faxoniana* regeneration had no preference on microsites. Compared to gap characteristics, microsites are more important for *A. faxoniana* regeneration.

Keywords: *Abies faxoniana*; bamboo; gap characteristics; microsites; tree regeneration

Introduction

Canopy gaps provide new openings for understory species (Wang & Liu 2011). The physical characteristics of gaps, such as gap size and age, directly affect the microclimate in gaps and contribute to the heterogeneity of microsites (Indra & Per 2009; 'microsite' in this work is understood as substrates where tree regeneration growing). For instance, gaps with various sizes may lead to distinct differences in seedling amounts and coexistence patterns among species (Caccia et al. 2009); with gap age increases, the understory light intensity decreases, the recruitment patterns of trees species change, and thus, species diversity varies with time (Zhang et al. 2013). Furthermore, under the influence of gap size and age, microsites and understory vegetation often exert important effects on the regeneration patterns of tree species (Taylor et al. 2006).

The influence of microsites on tree regeneration varies among substrates (fallen logs, stumps, rocks, soil, etc.) and changes with the interspecific competition (Mori et al. 2004). For example, since high-bamboo cover has significantly negative effects on seedling density (Guo et al. 2013), some coniferous trees regenerate more on decaying logs and stumps where their competitions with bamboos are less severe (Taylor et al. 2006). However, these raised microsites may be more important for light-demanding species or small-seeded species (Taylor et al. 2006). As a gap-dependent and large-seeded shade-tolerant species (Yan et al. 2012), *Abies faxoniana* (Rehd. et Wils.) has high requirement for short longevity. Artificial regeneration is typically necessary for this

species. Then, the question is what kind of microsites is more favorable for the regeneration of *A. faxoniana* in sites with dense bamboos?

A. faxoniana coniferous forests are widely distributed in the eastern margin of the Qinghai–Tibet Plateau, the highest plateau on the earth. The subalpine coniferous forest dominated by this tree species plays an important role in water conservation by preventing soil erosion and in keeping the Giant Panda habitats stable (Wu et al. 2011). For example, in southwestern Sichuan in China, *A. faxoniana* is present over the entire altitudinal range in Wanglang Giant Panda Reserve (Zhao et al. 2012). *A. faxoniana* seedling and sapling banks determine the population size of this species and strongly influence the succession and restoration of the forests. In these forests, raised microsites often cover only a small percent (<10%) of the forest ground, whereas the most widespread microsites are moss-cover ground and bare soil bed. Thus, is it possible that the raised microsites exert little effect on *A. faxoniana* regeneration, while moss-cover ground and bare soil bed may play important role?

This study aimed to clarify the effects of gap size and age on *A. faxoniana* recruitment on 4 typical microsites (bare soil bed, moss-cover ground, decaying logs, and stumps) in 97 gaps with or without dwarf bamboo (*Fargesia denudata* Yi), with the following specific objectives:

- (1) Will the increase in gap size reduce the densities of *A. faxoniana* seedlings and saplings on four microsites in the gaps with and without bamboo cover?

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- (2) What are the effects of gap age on the occurrences of *A. faxoniana* seedlings and saplings on four microsites in the gaps with and without bamboo cover?
- (3) Under the influence of gap size and age, what kind of microsites is favorable for *A. faxoniana* regeneration in gaps with and without bamboo cover?

Methods

Study site

Our studied area is located in an old-growth *A. faxoniana* forest in Wanglang Natural Reserve (31° 43′–33°03′ N, 103° 49′–104° 59′ E; altitude: 2300–4980 m) in south-western China. The average temperature is 11–17.5°C in July and –6~1°C in January. The mean annual precipitation is around 1100 mm (Zhao et al. 2012). The main soil type is mountain brown dark coniferous forest soil. The main associated tree species are *Sabina saltuaria* (Rehd. et Wils.) and *Betula utilis* (D. Don). Shrubs are mainly *Lonicera maackii* (Rupr.), *Rosa davidii* (Crep. Var. Davidii), *Sorbus koehneana* (Schneid.), etc. Dwarf bamboo, *F. denudata*, is another dominant understory plant in Wanglang (Taylor et al. 2006).

Plot setting and sampling

In this study, 10 located transect belts (20 × 100 m for each; with the similar altitude, slope, and aspect) were established randomly on Dawodang in Wanglang Natural Reserve. Gaps in transecting belts were recorded. In each gap, one plot in each quadrant (north, west, south, and east) and one another plot at the gap center were set. The sizes of the plots in gaps varied between 4 and 100 m², ranging from 4 to 16 m² for small-sized gaps (50–200 m²), from 16 to 64 m² for medium-sized gaps (200–1000 m²), and from 64 to 100 m² for large-sized gaps (1000–2000 m²; Zhang et al. 2013). The longitude, latitude, altitude, slope, aspect, size, and age of each gap were recorded at the gap center. Gap size was determined by subdividing the gaps into triangles and then measuring and adding the areas of the triangles (de Lima 2005). Gap age was calculated according to the degree of

decomposition of the trees that fell and created the gap (Table 1; Schnitzer & Carson 2001). Meanwhile, the length, diameter of each log, and stump in these plots were also measured. The decomposition grades of logs were recorded according to the eight-grade scale (Liu & Hytteborn 1991; Kirchner et al. 2011). Besides, the number, height, and recruitment microsites (bare soil bed, moss-cover ground, decaying logs, or stumps) of *A. faxoniana* seedlings and saplings, as well as the number, coverage, and height of *F. denudata*, were counted in each plot. *A. faxoniana* seedlings or saplings were classified as follows: seedlings, ≥10 and <50 cm in height; saplings, ≥50 cm in height and <5 cm in DBH (Zhao et al. 2012).

A total of 103 gaps were recorded in the studied area, ranging from 20 to 1860 m² in size and 2–60 years in age, and a total of 515 plots were recorded. During the later analyses, we classified these gaps into three size classes (I: <200 m² [‘small’], II: 200–1000 m² [‘medium size’], and III: 1000–2000 m² [‘large’]) and three age classes (I: <20 years old [‘young’], II: 20–40 years [‘medium age’], and III: 40–60 years [‘old’]; Liu & Hytteborn 1991). The small gaps accounted for 72% of the total gaps, while the medium-sized gaps were around 26% and the large gaps were less than 3%, the corresponding shares according to gap area were 27.4%, 61.7%, and 10.9%, respectively; the medium-aged gaps accounted for the largest proportion of gaps (50.49%), while the young gaps accounted for 23.30% and the old gaps accounted for 26.21%. Later, the 103 gaps were classified into four types: A gaps, having *A. faxoniana* recruitment without *F. denudata*; F gaps, having *F. denudata* without *A. faxoniana* recruitment; AF gaps, having both *A. faxoniana* recruitment and *F. denudata*; and N gaps, having neither *A. faxoniana* recruitment nor *F. denudata*. Only A and AF gaps were used in analysis about *A. faxoniana*, while F and AF gaps were used to compare the characteristics of *F. denudata*. In specific, since 6 gaps were N gaps, only 97 gaps were included in the later analyses, and only 485 plots were valid. Besides, since it is possible that some of these AF gaps may develop into F gaps with time, the current investigation may be useful for future work.

Table 1. The decomposition degrees used for the estimation of log and gap ages (Liu & Hytteborn 1991).

Part	Age (year)	Class	Description
Crown	1–2	I	Most of the leaves/needles remain on branches; some of them are still green.
	3–5	II	Most of the fine twigs remain; some of them have yellow leaves.
	6–10	III	Without leaves; a few fine twigs left; most of the bark remains; the wood is still hard and not rotten.
	11–20	IV	Without fine twigs, but main branches remain, supporting the trunk; small areas are covered by bark; wood has started to rot.
Trunk	21–30	V	Trunk has rotted to 1–2 cm depth and a knife can penetrate the wood.
	31–40	VI	Trunk lies on the ground or is supported by very thick branches, rotten wood 5–10 cm; a knife can easily penetrate the wood; the branches disconnect from the trunk and can easily be moved by hand.
Log	41–50	VII	Whole log is rotten, almost no branches; log still was kept in the form of a cylinder.
	51–60	VIII	Whole log is very soft and has sunk to half of the original diameter or more. It may easily be crushed with the foot.
	61–70	>VIII	Almost disappeared, some fragments could be found under the bryophyte layer.

In our studied area, the moss-cover ground is the most widely distributed, followed by the bare soil bed, while the decaying logs and the stumps were rare. Three hundred and twenty-one logs with the mean diameter at larger end of 0.32 ± 0.25 m and with the mean covering area of 1.99 m² were recorded. Twenty-one stumps were recorded (mean height of 0.53 ± 0.29 m and mean basal area of 0.19 m²). In general, the area proportion of each microsite was similar in different gaps: moss-cover ground occupied 81.62% of the forest floor, bare soil bed occurred 15.60%, while decaying logs and stumps occupied only 2.51% and 0.27%, respectively (Table 2).

Data analysis

Analysis of variance and least-significance-difference method (when equal variances assumed), Kruskal–Wallis H nonparametric test and Games–Howell post hoc test (when equal variances were not assumed) were applied to certify the statistically significant differences (Figures 1–4). However, since the data of large A gaps were null, independent samples test and Mann–Whitney U test were also used (Figures 1 and 2). All statistical analyses were performed using R-2.11 software (<http://www.R-project.org/>). Graphs were drawn using GraphPad Prism.

Results

Effects of gap size on densities of *A. faxoniana* recruitment among four microsites in A versus AF gaps

In both A and AF gaps, *A. faxoniana* seedlings and saplings occurred most frequently in small gaps (<200 m²; $P < 0.05$; Figures 1 and 2).

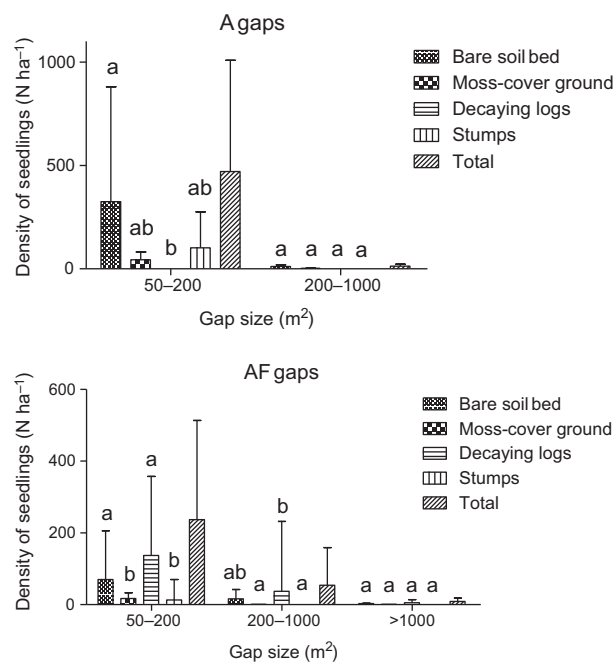


Figure 1. Densities (number/area, mean \pm SD, ha⁻¹) of *A. faxoniana* seedlings per microsite on bare soil bed, moss-covered ground, decaying logs, and stumps in three sized A and AF gaps in Wanglang Natural Reserve, southwestern China. Note: Different lower case letters denote significant differences among four microsites in the same sized gaps ($P < 0.05$).

- (1) Seedlings: the densities of *A. faxoniana* seedlings showed significant differences among microsites. First, in term of gap size, no matter whether it was in A or AF gaps, the seedling number on each microsite was not significantly decreased with the gap size increased ($P > 0.05$).

Table 2. The averaged area proportions (%) of bare soil bed, moss-cover ground, decaying logs, and stumps in three-sized and aged A, F, and AF gaps in Wanglang Natural Reserve, southwestern China.

Gap type		Bare soil bed	Moss-cover ground	Decaying logs	Stumps	Total
A gaps	Gap size					
	50–200 m ²	0.71	96.52	2.00	0.77	100.00
	200–1000 m ²	3.67	93.33	3.00	0.00	100.00
	>1000 m ²	0.00	0.00	0.00	0.00	0.00
	Gap age					
	<20 years	3.00	92.00	4.33	0.67	100.00
20–40 years	0.00	98.52	0.80	0.68	100.00	
40–60 years	3.50	93.50	3.00	0.00	100.00	
F gaps	Gap size					
	50–200 m ²	16.00	81.72	2.14	0.14	100.00
	200–1000 m ²	42.67	53.90	3.33	0.10	100.00
	>1000 m ²	77.00	21.00	2.0	0.0	100.00
	Gap age					
	<20 years	17.50	78.75	3.75	0.00	100.00
20–40 years	14.00	85.67	0.00	0.33	100.00	
40–60 years	51.25	45.67	3.00	0.08	100.00	
AF gaps	Gap size					
	50–200 m ²	2.29	95.31	2.32	0.08	100.00
	200–1000 m ²	3.71	93.35	2.93	0.01	100.00
	>1000 m ²	33.70	59.90	4.70	1.70	100.00
	Gap age					
	<20 years	0.76	96.88	2.12	0.24	100.00
20–40 years	3.18	94.64	2.15	0.03	100.00	
40–60 years	7.79	88.46	3.68	0.07	100.00	

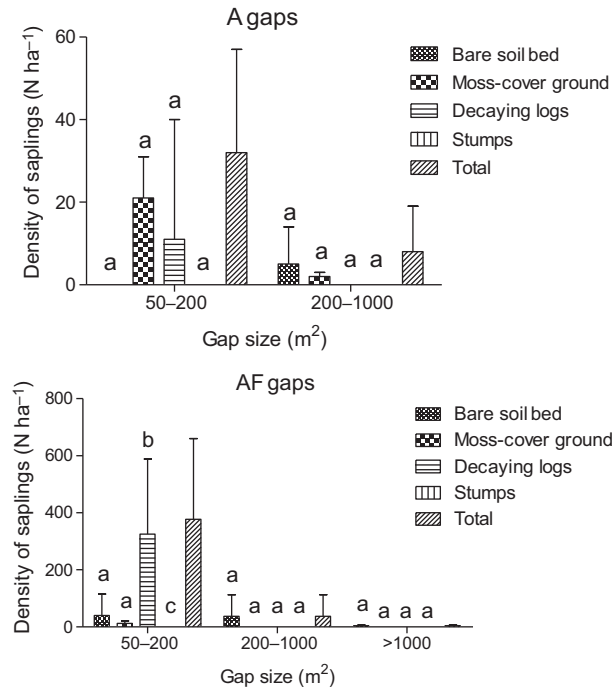


Figure 2. Densities (number/area, mean \pm SD, ha^{-1}) of *A. faxoniana* saplings per microsite on bare soil bed, moss-cover ground, decaying logs, and stumps in three sized A and AF gaps in Wanglang Natural Reserve, southwestern China. Note: Different lower case letters denote significant differences among four microsites in the same sized gaps ($P < 0.05$).

Second, in term of microsites, in small A gaps, the densities of *A. faxoniana* seedlings on bare soil bed were significantly higher than those on decaying logs ($P < 0.05$). On the contrary, in small- and medium-sized AF gaps, *A. faxoniana* seedlings were more abundant on decaying logs and bare soil bed ($P < 0.05$; Figure 1).

- (2) Saplings: first, in term of gap size, in both A and AF gaps, the *A. faxoniana* sapling numbers on moss-cover ground significantly decreased with the increase in gap size ($P < 0.05$). Similarly the sapling numbers on decaying logs significantly decreased with the sizes of AF gap increased ($P < 0.05$). In contrary, the sapling densities on other microsites varied insignificantly ($P > 0.05$). Second, in term of microsites, in small AF gaps, *A. faxoniana* saplings occurred most frequently on decaying logs ($P < 0.05$). However, in A gaps and in medium size and large AF gaps, *A. faxoniana* saplings were rarely seen on the four microsites ($P > 0.05$; Figure 2).

Effects of gap age on *A. faxoniana* recruitment densities among four microsites in A versus AF gaps

In AF gaps, *A. faxoniana* saplings were more abundant in young (<20 years) and medium-aged gaps (20–40 years) than in old gaps (40–60 years; $P < 0.05$). However, the sapling densities in A gaps and the seedling densities varied insignificantly with the gap age ($P > 0.05$; Figures 3 and 4).

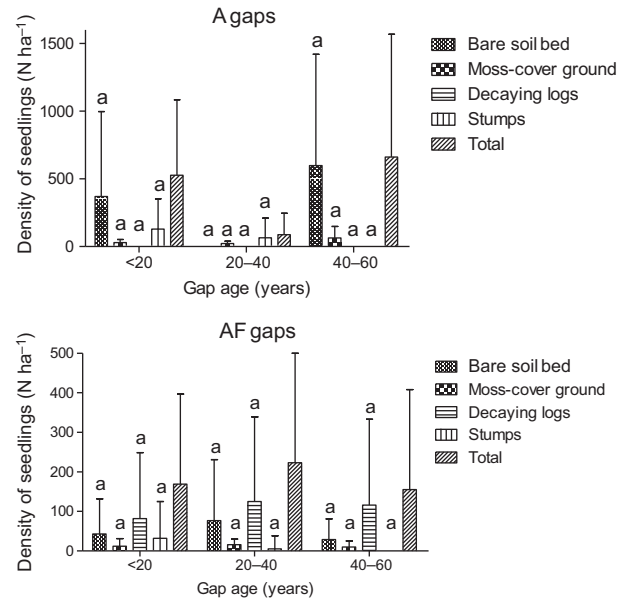


Figure 3. Densities (number/area, mean \pm SD, ha^{-1}) of *A. faxoniana* seedlings per microsite on bare soil bed, moss-cover ground, decaying logs, and stumps in three aged A and AF gaps in Wanglang Natural Reserve, southwestern China. Note: Different lower case letters denote significant differences among four microsites in the same sized gaps ($P < 0.05$).

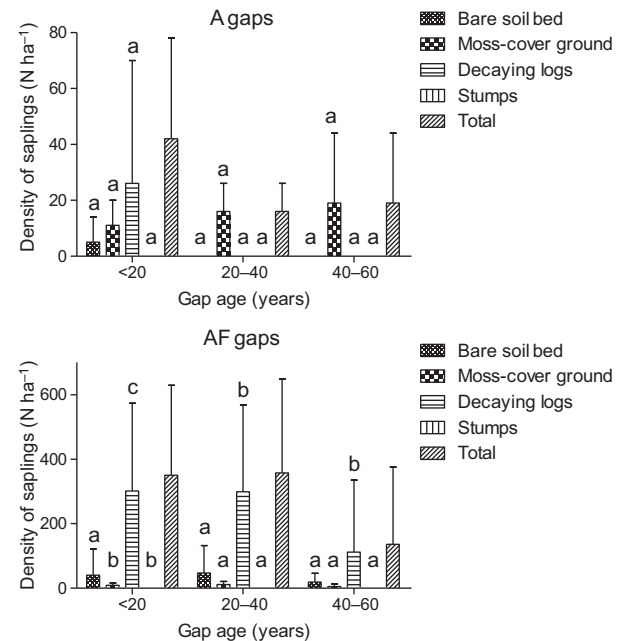


Figure 4. Densities (number/area, mean \pm SD, ha^{-1}) of *A. faxoniana* saplings per microsite on bare soil bed, moss-cover ground, decaying logs, and stumps in three aged A and AF gaps in Wanglang Natural Reserve, southwestern China. Note: Different lower case letters denote significant differences among four microsites in the same sized gaps ($P < 0.05$).

- (1) Seedlings: first, in term of gap age, in both A and AF gaps, the seedling density in each microsite varied irregularly with the gap age ($P > 0.05$). Second, in term of microsites, in medium-aged and old AF gaps, *A. faxoniana*

seedlings were more abundant on decaying logs and bare soil bed ($P < 0.05$). However, in A gaps as well as in young AF gaps, the *A. faxoniana* seedling densities barely differed among microsites ($P > 0.05$; Figure 1).

- (2) Saplings: first, in term of gap age, increased gap age barely influenced the sapling densities in A gaps ($P > 0.05$). However, in AF gaps, the sapling numbers on decaying logs were significantly decreased with the gap age increased ($P < 0.05$), while *A. faxoniana* saplings on other microsites were rare ($P > 0.05$). Second, in term of microsites, the densities of *A. faxoniana* saplings in A gaps were not significantly different among microsites ($P > 0.05$). However, in each aged AF gap, *A. faxoniana* saplings occurred most frequently on decaying logs ($P < 0.05$; Figure 2).

Discussion

Environmental heterogeneity in forests plays an important role in the establishment and growth of tree regeneration. In subalpine coniferous forests, gap formation and microsite heterogeneity are thought to be a key for tree regeneration (Royo & Carson 2008). In some forests, specific microsites are more important than gap characteristics (Nakashizuka 1989), as indicated in this study: the seedling and sapling densities of *A. faxoniana* significantly varied among microsites while barely impacted by gap size and age, except that increased gap size and age significantly reduced the sapling densities on moss-cover ground and decaying logs.

With regarding to the first question, our study only indicates the significant inhibition of the increased gap size on the sapling densities on moss-cover ground and decaying logs. Unfavorable environment for the establishment and growth of saplings in large gaps is obvious on moss-seedbed (which in our study areas include moss-cover ground and decaying logs; Zhang et al. 2013). Increased solar irradiation and soil temperatures accelerate the desiccation of tree regeneration (Darabant et al. 2007). Drying of moss-seedbed in large gaps could be at least two times faster than under the canopies (Tanskanen et al. 2006).

With respect to the second question, the results confirm that gap age exerted a significantly negative effect on the sapling densities on decaying logs in AF gaps. It implied that the importance of decaying logs for saplings may gradually reduce with time. As described by Bace et al. (2012), with the decaying logs become more rotten, these raised surfaces get closer to the forest ground, the litter layer is increasingly thicken (Harmon & Franklin 1989), and thereafter the positive effect of surrounding plants turns to be the negative one. Meanwhile, if sapling roots do not reach the forest ground, decaying logs would also be increasingly instable and lack of nutrients (Brang et al. 2003). All these changes would contribute to an unfavorable environment on decaying logs.

With regarding to the third question, both bare soil bed and decaying logs may be favorable for *A. faxoniana* regeneration. On the one hand, the positive role of decaying logs is obvious. Decaying logs with moss layer provide moist environment for seedling growth and survival, especially in summer (Iijima & Shibuya 2010). However, *A. faxoniana* saplings obviously preferred to establish on decaying logs in AF gaps, while distributed relatively evenly among different microsites in A gaps. It implied that only with bamboos growing nearby would the *A. faxoniana* saplings rely on decaying logs to regenerate. On the other hand, although bare soil bed may be drier than other microsites, our results prefer to confirm that *Abies* can be well established on both rotten wood seedbeds and forest floor (Eastham & Jull 1999).

It has been known that seed size is a key factor related to differential microsites colonization among tree species (Christie & Armesto 2003). Many coniferous species, mainly the small-seeded species such as *Picea* spp. and *Tsuga* spp. (Bace et al. 2012), usually rely on elevated surfaces to successfully regenerate (Iijima & Shibuya 2010). In contrast, larger-seeded species, such as *Abies* spp., with longer tap roots and longer shoots, are resistant to various stresses and generally do not require very specific substrates (Arbour & Bergeron 2011). This may explain our results which support that *Abies* can regenerate on soil and moss-cover ground as well as on decaying logs and stumps.

Conclusion

This study has provided lines of evidence that *A. faxoniana* seedlings and saplings could regenerate on moss-cover ground and bare soil bed as well as on decaying logs and stumps. Microsites in A gaps are not so important for *A. faxoniana* regeneration as they are in AF gaps. In addition, gap size and age do not affect the preference of *A. faxoniana* regeneration on microsites. Furthermore, some other factors might affect the establishment and growth of *A. faxoniana* regeneration as well. In further studies, more gap characteristics should be considered into studies on the competition between tree regeneration and bamboos. More attention should also be paid to the detailed mechanisms of *Abies* spp. to establish on specific substrates.

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