Forest Systems
24(2), e025, 9 pages (2015)
eISSN: 2171-9845
http://dx.doi.org/10.5424/fs/2015242-06682
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)

RESEARCH ARTICLE

OPEN ACCESS

Effects of gap size, gap age, and bamboo *Fargesia denudata* on *Abies faxoniana* recruitment in South-western China

Wen Kang[1], Cheng Tian[1], Dongwei Kang[1], Mengjun Wang[2], Yunxi Li[3], Xiaorong Wang[3] and Junqing Li [1,*]

[1] The Key Laboratory for Silviculture and Conservation of Ministry of Education, Beijing Forestry University, Beijing 100083, P. R. China. [2] Kunming Survey and Design Institute of State Forestry Administration, Kunming, 650216 China. [3] Wanglang Natural Reserve, Pingwu County, Mianyang, Sichuan 622550, China

Abstract

Aim of study: to study the effects of gap size, gap age and bamboo *Fargesia denudata* on natural regeneration of *Abies faxoniana*, both of which are the ubiquitous dominants in our research area.

Area of study: subalpine coniferous forests in Wanglang Natural Reserve in Southwestern China.

Material and Methods: 10 transect belts were randomly established, and a total of 97 gaps were recorded and used.

Main results: (1) the number of bamboos with coverage of <17% significantly increased with increases of gap size and age, but the latter had little influence on the numbers of *F. denudata* with coverage of >17%. (2) *F. denudata* strongly inhibited *A. faxoniana* seedlings and saplings in small, young and old gaps, where the amount of *A. faxoniana* recruitment was relatively abundant, than in other types of gap. (3) The numbers of *A. faxoniana* seedlings in A-gaps, significantly decreased with the increases in gap size. However, in gaps where *F. denudate* was also present, *A. faxoniana* seedlings and saplings were insensitive to gap size or age. *Research highlights*: thick *F. denudata* would not be influenced by gap size or age. Because of the low occurrences of *A. faxoniana* seedlings and saplings, the negative effect of gap size, gap age and *F. denudata* on *A. faxoniana* recruitment was unclear

Keywords: *Abies faxoniana*; *Fargesia denudata*; gap age; gap size; regeneration.

Citation: Kang, W., Tian, C., Kang, D., Wang, M., Li, Y., Wang, X., Li, J. (2015). Effects of gap size, gap age, and bamboo *Fargesia denudata* on *Abies faxoniana* recruitment in South-western China. Forest Systems, Volume 24, Issue 2, e025, 9 pages. http://dx.doi.org/10.5424/fs/2015242-06682.

Received: 15 Aug 14. **Accepted**: 01 Feb 2015

Funding: This work is supported by Special Research Program for Public-welfare Forestry Protection Projects (201404422) and 111 Project (B13007).

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Junqing Li: lijq010@gmail.com

Introduction

Canopy gaps, known as spatial and temporal environmental heterogeneity in forests (Denslow, 1987; Connell, 1989; Ostertag, 1998), facilitate the establishment and growth of understory vegetation (Ehrenfeld, 1980; Huenneke, 1983) by creating new open spaces and releasing resources (Gray & Spies, 1997; McGuire *et al*., 2001; De Chantal *et al*., 2003). Gaps are favorable not only for light-demanding species like bamboos and shrubs (Taylor & Qin, 1988a), but also for shade-tolerant coniferous regeneration as well (Gaudio *et al*., 2008). The crucial effect of gap characteristics on the understory plants has been reported in many studies (e.g. Runkle, 1985; Takahashi, 1997; Narukawa & Yamamoto, 2001). For one thing, gap size is thought to be very important in maintaining the species diversity and tree regeneration success (Brokaw, 1985; Pearson *et al*., 2003; Li *et al*., 2005; Albanesi *et al*., 2008). For example, higher light availability in large gaps primarily facilitates coniferous regeneration's competitors, e.g. shrubs, broad - leaved tree seedlings, and bamboos (Sapkota & Oden, 2009), which would reduce the light received by coniferous regeneration. Moreover, large gaps reduce soil moisture and raise the air temperature, and therefore increase the mortality of young seedlings (Darabant *et al*., 2007). For another, gap age, which is known as gap phase or temporal heterogeneity of gap disturbance, directly relates to the microsite situations and consequently influences on the establishment and growth of understory vegetation (Barik *et al*., 1992; Chandrashekara & Ramakrishnan, 1994; Kirchner *et al*., 2011; Kinny *et al*., 2012; Zhang *et al*., 2013). With the gap environment develops, the gradually lower light levels would lead to inter-species competing for light (Bullock, 2000), and consequently hinder the establishment of seedlings and saplings. To clarify, gap environments determined by various gap characteristics usually contribute to different species coexistence patterns underneath.

Moreover, it is widely reported that the light-demanding species, such as shrubs and bamboos, play major roles in shaping the recruitment pattern of canopy trees (e.g. Rousset & Lepart, 2000; Griscom & Ashton, 2003; Campanello *et al*., 2007; Tsvuura *et al*., 2010). Bamboos, for instance, greatly inhibit tree seedlings and saplings in many forests in Japan (Nakashizuka, 1989; Yamamoto, 1995), China (Taylor *et al*., 2006), Chile (Veblen, 1989), the United States (Harmon & Franklin, 1989), etc. Because of their rapid clonal growth and high degree of dominance (Nakashizuka & Numata, 1982a, b; Veblen, 1982; Lusk, 2001; Wang *et al*., 2006), bamboos largely reduce the underneath light availability, as well as the nutrients and water in soil (Rao & Ramakrishnan, 1989; Singh & Singh, 1999; Beckage & Clark, 2003; Takahashi *et al*., 2003; Embaye *et al*., 2005; Tripathi *et al*., 2005; Montti *et al*., 2011), and therefore, diminish the seedling abundance of the surrounding trees (Nakashizuka, 1988; Beckage *et al*., 2000; Caccia *et al*., 2009; Larpkern *et al*., 2010). Although much relevant research has been done, it will be interesting to add the influence of gap characteristics into the relationship between bamboos and tree regeneration. In this respect, a subalpine conifer forest can be regarded as a suitable research site.

The subalpine coniferous forest is of important ecological and economic value in many countries, such as Chile (Veblen *et al*., 1981; Gonzalez *et al*., 2002), North America (Runkle, 1981), Japan (Nakashizuka, 1987; Yamamoto, 1993; Narukawa & Yamamoto, 2002), and China (Taylor & Qin, 1988b; Taylor *et al*., 1996; Liu & Wu, 2002; Dang *et al*., 2010; Guo *et al*., 2013). Take the one selected in Southwestern China for example, *Abies faxoniana* Rehd. et Wils. is the dominant tree species and bamboo *Fargesia denudata* is an understory dominant. Where this dwarf bamboo is dense, the seedlings and saplings of *A. faxoniana* are often scarce and concentrated on raised surfaces (Holz & Veblen, 2006; Taylor *et al*., 2006). Based on these observations, the aim of this work was to study the effects of gap size, gap age and *F. denudata* on *A. faxoniana* seedlings and saplings. For this purpose, we randomly established 10 transect belts located in the Wanglang Natural Reserve, and then inventoried the number, coverage of *F. denudata*, as well as the numbers of *A. faxoniana* seedlings and saplings in 97 natural formed gaps. We tried to elucidate the following issues:

(1) Whether the gap size and age would influence the numbers and coverage of *F. denudata*?
(2) What are the effects of gap size and age for *A. faxoniana* seedlings and saplings in gaps with bamboos?
(3) What are the effects of *F. denudata* for *A. faxoniana* seedlings and saplings in different sized or aged gaps?

Methods

Layout of the study area

This study was conducted in old-growth *Abies faxoniana*-*Picea purpurea* mixed forests in Wanglang Natural Reserve in southwestern China, which covers a total area of 325 km^2 (31^{o}43'-33^{o}03' N, 103^{o}49'-104^{o}59' E, altitude 2,300-4,980 m). The mean annual temperature is 11.4-16.8 ^{o}C, and the mean annual temperature sum (with daily temperature above 0 ^{o}C) is about 5,366.6 d.d. The mean annual precipitation is about 1,100 mm, and 58.51% of the annual precipitation takes place from May to September (Zhao *et al*., 2012).

The study area situated in a typical subalpine coniferous forest in Wanglang Natural Reserve. The terrain is steep and dissected. Limestone is the main parent material, and mountain brown dark coniferous forest soil is the dominant soil type in our study area. The typical vegetation is *A. faxoniana-Picea purpurea* forest associated with *Sabina saltuaria*, *Betula utilis* and *F. denudata*, etc., and with a ground cover of mosses and grasses (Taylor *et al*., 2006). The shrub layer mainly consists of *Lonicera maackii*, *Rosa davidii* Crep. Var. Davidii, and *Sorbus Koehneana* Schneid. The herb layer is comprised of Asteropyrum, Kingdonia, etc. The dominant mosses in forests are mostly Pottiaceae, Plagiomnium, Brachytheciaceae, and Hylocomiaceae (Li *et al*., 2012). Based on our previous studies, the mean stand height and diameter at breast height (D.B.H.) of *A. faxoniana* trees in our studied areas are 17 m and 20.4 cm, respectively. The stand density is 950 trees N/ha, and the basal area is between 14.8 and 25.7 m^2/ha. The ages of the *A. faxoniana* trees ranged from 60 to 230 years.

Field measurements and data analyses

To study the effects of gap size and age on *A. faxoniana* recruitment and *F. denudata*, 10 located transect belts were established in Wanglang from May to June in 2013. The transects (20 m × 100 m for each) were established randomly but in regions with the same altitude, slope and aspect. We also recorded those gaps which distributed near the transect belts (no more than 20 m in distance). In each transect belt, we recorded the sizes and ages of the gaps. The size of each gap was determined by subdividing the irregularly shaped gaps into smaller sections and then measuring each section (de Lima, 2005). Gap age was calculated from the degree of decomposition of the gap makers (Liu & Hytteborn, 1991; Schnitzer & Carson, 2001).

Each gap was divided diagonally into four quadrants (east, north, west, south), then 4 subplots were randomly set in these quadrants and another subplot was selected at the center of the gap. The sizes of sampled plots in small gaps varied from 4 m^2 to 16 m^2, in medium-size gaps varied between 16 and 49 m^2, while in large gaps varied between 49 and 100 m^2 (Zhang *et al.*, 2013). Longitude, latitude, altitude, slope and aspect of each gap were recorded at the gap center. The length and diameter of logs, and stumps were also measured. The decomposition grades of logs were recorded according to the eight-grade scale (Liu & Hytteborn, 1991; Kirchner *et al.*, 2011). Meanwhile, in each quadrant plot, the number of *A. faxoniana* regeneration, and the number and coverage of *F. denudata*, were recorded. *A. faxoniana* regeneration was classified into two size classes: seedling and sapling (seedlings: ≥ 10 cm and <50 cm in height; saplings: ≥ 50 cm in height and < 5 cm in DBH) (Zhao *et al.*, 2012).

Data analysis

A total of 103 naturally formed gaps were recorded, with sizes ranging from 20 to 1,860 m^2 and ages from 3 to 60 years. However, since 6 gaps had neither *A. faxoniana* regeneration nor *F. denudata*, only 97 gaps were used during the later analyses. The 97 gaps were then classified into three gap size classes [I: < 200 m^2 ('small'), II: 200-1,000 m^2 ('medium-size'), and III: 1,000-2,000 m^2 ('large')], and three gap age classes [I: < 20 years old ('young'), II: 20-40 years ('medium-age'), and III: 40-60 years ('old')] (Liu & Hytteborn, 1991). Meanwhile, in order to analyze the effects of bamboos on *A. faxoniana* recruitment, the 97 gaps were classified into four types: A-gaps, having *A. faxoniana* recruitment without *F. denudata*; Sn-gaps, gaps with *F. denudata* cover < 17%; Ss-gaps, gaps with *F. denudata* cover >=17%; and F-type gaps, having *F. denudata* without *A. faxoniana* recruitment. Plant density was recorded as N/m^2, and afterwards converted into N/ha for analysis. ANOVA and LSD post hoc tests (when equal variances assumed), or Kruskal-Wallis H nonparametric tests and Games-Howell post hoc tests (when equal variances not assumed) were applied in this work to certify the statistically significant differences. All statistical analyses were performed using R-2.11 software (http://www.R-project.org/).

Results

Effects of gap size and age on the characteristics of *F. denudata*

Firstly, gap size exerted important effect on *F. denudata* in Sn-gaps while it had little effect on *F. denudata* in Ss-gaps and F-gaps. It was clear that the numbers and coverage of *F. denudata* significantly increased as the Sn-gaps got larger ($p<0.05$; Figure 1). However, no matter what the gap size was, the numbers and coverage of *F. denudata* in Ss-gaps and F-gaps were constantly high

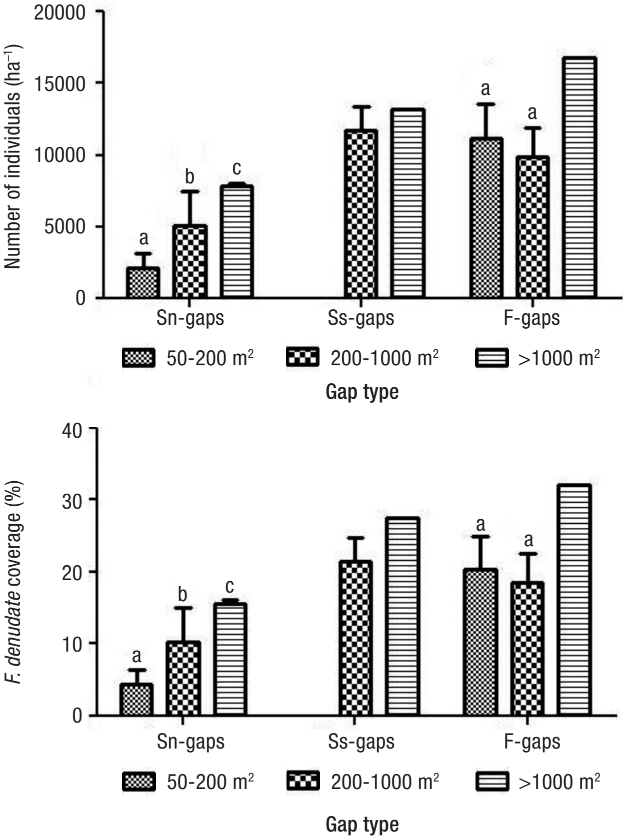

Figure 1. Numbers (mean±S.D., ha^{-1}) and coverage (mean±S.D., %) of *F. denudata* in three sized gaps. Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%; F-gaps: gaps having *F. denudata* without *A. faxoniana* recruitment.
Note: Different lower case letters denote significant differences among gaps with the same type but different sizes ($p < 0.05$). The Kruskal - Wallis H nonparametric test and Games –Howell post hoc test were used in order to compare the numbers and coverage of *F. denudata* in three sized Sn-gaps. The Independent samples test was also used to compare the numbers and coverages of *F. denudata* in small and medium -size F-gaps.

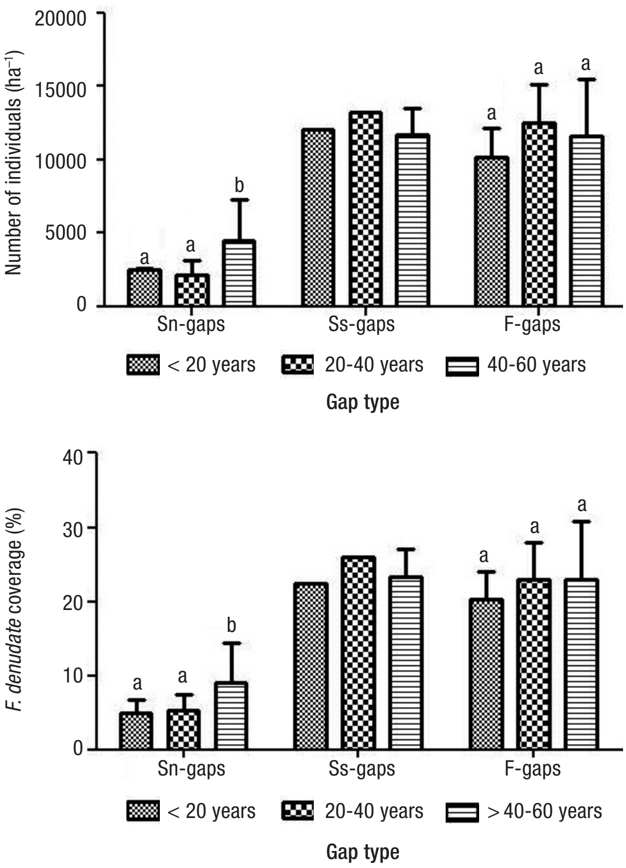

Figure 2. Numbers (mean±S.D., ha^{-1}) of *F. denudata* in three aged gaps. Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%; F-gaps: gaps having *F. denudata* without *A. faxoniana* recruitment

Note: Different lower case letters denote significant differences among gaps with the same type but different ages (p < 0.05). The Kruskal - Wallis H nonparametric test and Games - Howell post hoc test were used in order to compare the numbers and coverage of *F. denudata* in three sized Sn-gaps and F-gaps.

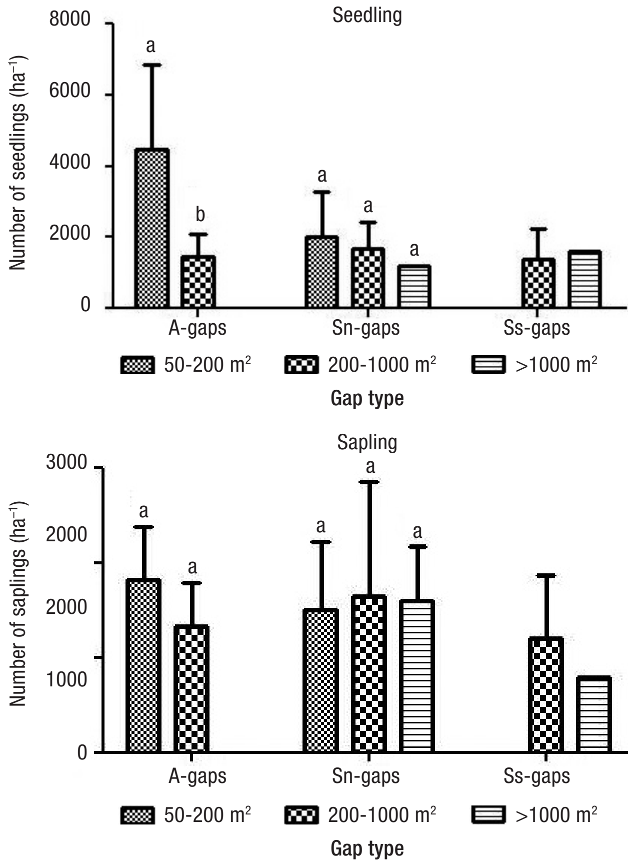

Figure 3. Effects of gap size on the numbers (mean±S.D., ha^{-1}) of *A. faxoniana* seedlings and saplings in gaps with different bamboo coverage. A-gaps: gaps having *A. faxoniana* recruitment without *F. denudata*; Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%.

Note: Different lower case letters denote significant differences among gaps with the same type but different sizes (p < 0.05). The Independent samples test was used to compare the numbers of *A. faxoniana* seedlings and saplings in small and medium-size A-gaps. ANOVA was used to compare the numbers of *A. faxoniana* seedlings and saplings in three sized Sn-gaps.

(p>0.05). Secondly, the numbers and coverage of *F. denudata* did not change obviously in young and medium-age Sn-gaps, however, when the gap ages increased from medium to old, the numbers and coverage of *F. denudata* in Sn-gaps increased significantly (p<0.05; Figure2). Similarly, the values of the two characteristics in each aged Ss-gap or F-gap were relatively constant (p>0.05).

Effects of gap size and bamboo on the recruitment numbers of *A. faxoniana*

Firstly, only the numbers of *A. faxoniana* seedlings in A-gaps decreased sharply with the increases of gap size (p<0.05), while those in Sn- or Ss-gaps, as well as the numbers of *A. faxoniana* saplings were not influenced by gap size (p>0.05; Figure 3). Secondly, the negative effect of *F. denudata* only occurred in small gaps: the occurrences of *A. faxoniana* seedlings in small Sn-gaps were significantly lower than in small A-gaps (p<0.05) (small Ss-gaps were not found). In contrast, no matter what the bamboo coverage was, *A. faxoniana* seedlings in medium-sized or large gaps, and *A. faxoniana* saplings generally were constantly scarce (Figure 4).

Effects of gap age and bamboo on the recruitment numbers of *A. faxoniana*

Firstly, gap age had little influence on the numbers of *A. faxoniana* seedlings and saplings (p>0.05; Figure 5). Secondly, it was only in young or old gaps that

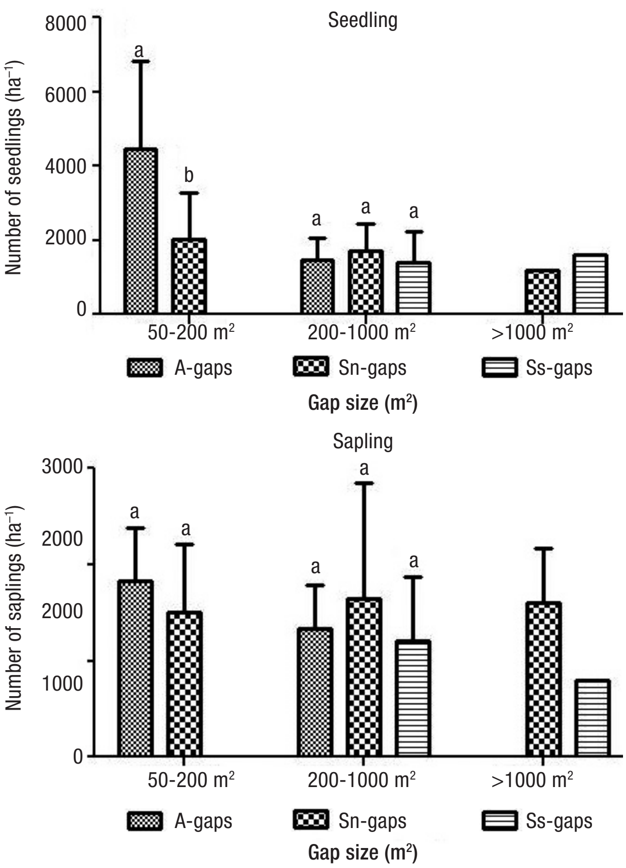

Figura 4. Bamboo effects on the numbers (mean±S.D., ha^{-1}) of *A. faxoniana* seedlings and saplings in three sized gaps. A-gaps: gaps having *A. faxoniana* recruitment without *F. denudata*; Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%.
Note: Different lower case letters denote significant differences among gaps with the same size but different types (p < 0.05). As for small gaps, the Mann-Whitney U test was used to compare the numbers of *A. faxoniana* seedlings between A-gaps and Sn-gaps, while the Independent samples test was used to compare the numbers *A. faxoniana* saplings between A-gaps and Sn-gaps. As for medium-size gaps, ANOVA was used in order to compare the numbers of *A. faxoniana* seedlings and saplings in A-gaps, Sn-gaps, and Ss-gaps. As for large gaps, since there was only no A-gap and only one Ss-gap, no statistical test was used in this group.

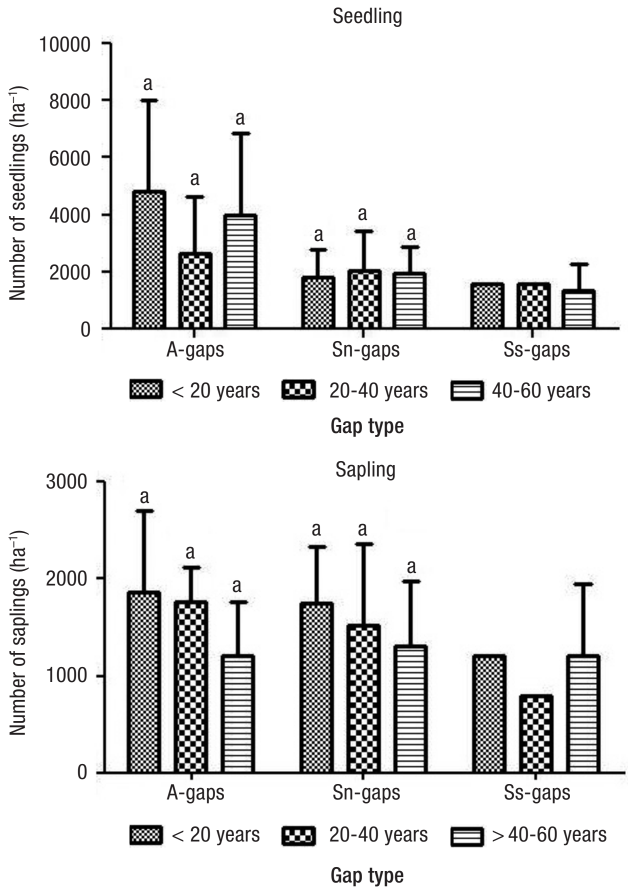

Figure 5. Effects of gap age on the numbers (mean±S.D., ha^{-1}) of *A. faxoniana* seedlings and saplings in gaps with different bamboo coverage. A-gaps: gaps having *A. faxoniana* recruitment without *F. denudata*; Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%.
Note: Different lower case letters denote significant differences among gaps with the same type but different ages (p < 0.05). ANOVA was used to compare the numbers of *A. faxoniana* seedlings and saplings in three aged A-gaps and Sn-gaps.

the numbers of *A. faxoniana* seedlings varied among A-, Sn-, and Ss-gaps ($p<0.05$). The numbers of *A. faxoniana* seedlings in young Sn-gaps were statistically lower than in young A-gaps ($p<0.05$) (the related data in Ss-gaps was insufficient for statistics). Similarly, the numbers of *A. faxoniana* seedlings in old Sn- and Ss-gaps were significantly lower than in old A-gaps ($p<0.05$). However, the numbers of *A. faxoniana* seedlings in medium-age gaps, as well as the numbers of *A. faxoniana* saplings barely varied ($p>0.05$; Figure 6).

Discussions

With regard to our first issue of whether the gap size and age would influence the *F. denudata* underneath, our study confirmed the numbers of *F. denudata* increased as the size or age of Sn-gaps increased. This finding is similar to the study on *F. qinlingensis* which also had higher densities in large gaps, and Wang *et al*. (2006) explained that increased light led to maturation of bamboos. We found that the succession of gaps may also benefit the clonal growth of bamboos. We also found that no matter the gap size or age, the numbers and coverage of *F. denudata* in Ss-gaps or F-gaps barely varied. It appears that the small amounts of bamboos, as in Sn-gaps, were stimulated by gap size and age. However, as for bamboos with a higher cover-

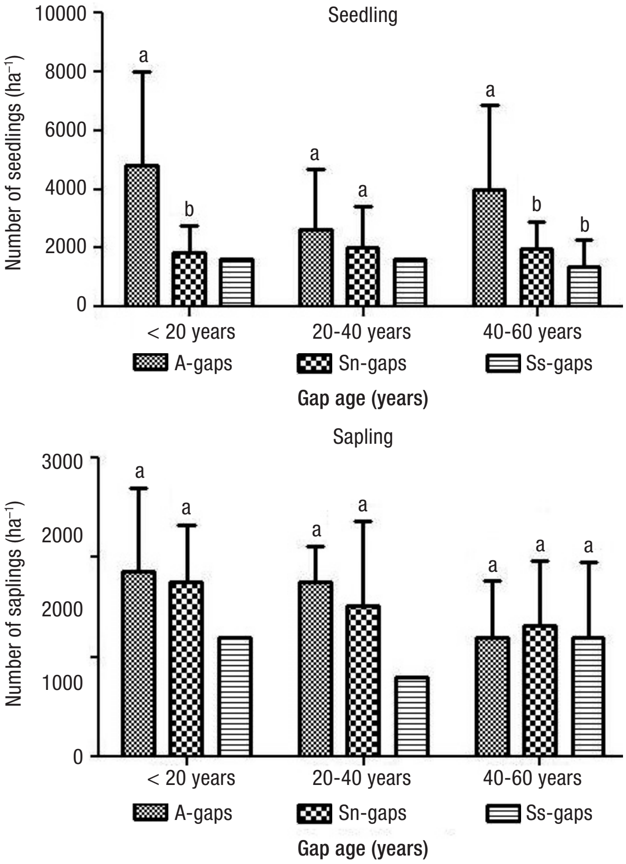

Figure 6. Bamboo effects on the numbers (mean±S.D., ha^{-1}) of *A. faxoniana* seedlings and saplings in three aged gaps. A-gaps: gaps having *A. faxoniana* recruitment without *F. denudata*; Sn-gap: gaps with *F. denudata* cover < 17%; Ss-gap: gaps with *F. denudata* cover >=17%

Note: Different lower case letters denote significant differences among gaps with the same age but different types ($p < 0.05$). As for young gaps, since there was only one Ss-gap, the Mann-Whitney U test was used in order to compare the numbers of *A. faxoniana* seedlings between A-gaps and Sn-gaps, while the Independent samples test was used to compare the numbers of saplings between A-gaps and Sn-gaps. As for medium-age gaps, the Independent samples test was used to compare the numbers of *A. faxoniana* seedlings and saplings between A-gaps and Sn-gaps. For old gaps, the Kruskal - Wallis H nonparametric test was used to compare the numbers of *A. faxoniana* seedlings in A-gaps, Sn-gaps and Ss-gaps, while ANOVA was used to compare the numbers of *A. faxoniana* saplings in A-gaps, Sn-gaps and Ss-gaps.

age, as in Ss-gaps and F-gaps, the positive effects of gap size and age got weaker. It implied that the niche of bamboos in larger or older gaps might be constrained by some other environmental variables, for example, topography and disturbance gradients, as well as canopy density and composition gradients which have been shown to influence the distribution and growth of dwarf bamboo, *F. nitida*, in subalpine forest in southwest China (Wang *et al*., 2009).

With respect to our second issue, our study denied the effects of gap size and age on the numbers of *A. faxoniana* seedlings and saplings in gaps with bamboos. The numbers of *A. faxoniana* seedlings in gaps without bamboos (A-gaps) significantly decreased with the increases of gap size. In general, in large gaps the establishment of tree regeneration will be limited by strong light radiation, high temperature and evaporation, and subsequently low soil water availability (Bullock, 2000; Zhang *et al*., 2013). However, *A. faxoniana* seedlings in gaps with bamboos (in Sn- and Ss-gaps) were insensitive to increased gap size, which may also result from the scarcity of *A. faxoniana* seedlings. Taylor *et al*. (2006) explained similarly that the importance of gap disturbance for Picea seedling establishment was not obvious because of the scarcity of Picea seedlings and saplings in their stands.

With regard to the third issue, our results proved the strong inhibition of *F. denudata* on *A. faxoniana* seedlings. In small, young and old gaps, the numbers of *A. faxoniana* seedlings were relatively abundant but sharply reduced with the increase of *F. denudata* coverage. The restraint of bamboos on conifer seedlings may results from the rapid growth and large biomass of bamboos (Taylor & Qin, 1989), and has been reported by many studies. For example, in forests in Chile, Japan, and Sichuan Province of China (e.g. Veblen *et al*., 1981; Runkle, 1981; Takahashi, 1994; Guo *et al*., 2013), dense bamboos occupy the forest understory or in canopy gaps and greatly impede tree seedlings and saplings. In addition, we found that in gaps with a small number of *A. faxoniana* seedlings or saplings, the effects bamboo was insignificant. The unclear effects of *F. denudata* coverage may also result from the low occurrence of *A. faxoniana* recruitment. After all, *A. faxoniana* is a fecund but short-lived species, with a high mortality of recruitment (Taylor *et al*., 2006).

Conclusion

Increased gap size and age would increase the numbers of *F. denudata* with low coverage. Where *A. faxoniana* seedlings were relatively abundant, *A. faxoniana* seedlings were significantly inhibited by increased gap size and *F. denudate*. In contrast, due to the low occurrences of *A. faxoniana* recruitment, gap size, gap age and *F. denudata* exerted little effect on *A. faxoniana* seedlings and saplings in gaps.

Moreover, whilst our findings are insufficient in sampling plots and investigation on gap size and age are inaccurate, this study could still provide useful information for research on gap characteristics, natural regeneration and the relationship between bamboos and tree recruitment in subalpine coniferous forests. In addition, more intensive study should be focused on the distances between conifer recruitment and understory bamboos, since the inhibition effects of bamboos on tree recruitment may directly depend on the distances between the two species.

Acknowledgments

We thank the Wanglang Natural Reserve for permission and their assistance in this investigation.

References

Albanesi E, Gugliotta OI, Mercurio I, Mercurio R, 2008. Effects of gap size and within-gap position on saplings establishment in silver fir stands. iFor Biogeosci For 1: 55-59

Barik SK, Pandey HN, Tripathi RS, Rao P, 1992. Microenvironmental variability and species-diversity in treefall gaps in a subtropical broadleaved forest. Vegetatio 103: 31-40

Beckage B, Clark JS, 2003. Seedling survival and growth of three southern Appalachian forest tree species: the role of spatial heterogeneity. Ecology 84: 1849-1861. http://dx.doi.org/10.1890/0012-9658(2003)084[1849:SSAGOT]2.0.CO;2

Beckage B, Clark JS, Clinton BD, Haines BL, 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Can J For Res 30: 1617-1631. http://dx.doi.org/10.1139/x00-075

Brokaw NVL, 1985. Gap-phase regeneration in a tropical forest. Ecol Lett 66: 682-687. http://dx.doi.org/10.2307/1940529

Bullock JM, 2000. Gaps and seedling colonization. In: Michael Fenner (ed). Seeds: The Ecology of Regeneration in Plant Communities. Wallingford, UK: CABI Publishing: 375-395. http://dx.doi.org/10.1079/9780851994321.0375

Caccia FD, Chaneton EJ, Kitzberger T, 2009. Direct and indirect effects of understorey bamboo shape tree regeneration niches in a mixed temperate forest. Oecologia 161: 771-780. http://dx.doi.org/10.1007/s00442-009-1412-z

Campanello PI, Gatti MG, Ares A, Montti L, Goldstein G, 2007. Tree regeneration and microclimate in a liana and bamboo-dominated Semi-deciduous Atlantic Forest. Forest Ecol Manag 252: 108-117. http://dx.doi.org/10.1016/j.foreco.2007.06.032

Chandrashekara UM, Ramakrishnan PS, 1994. Successional patterns and gap phase dynamics of a humid tropical forest of the Western Ghats of Kerala, India: ground vegetation, biomass, productivity and nutrient cycling. For Ecol Manag 70: 23-40.

Connell JH, 1989. Some processes affecting the species composition in forest gaps. Ecology 70: 560-562. http://dx.doi.org/10.2307/1940205

Dang HS, Zhang YJ, Zhang KR, Jiang MX, Zhang QF, 2010. Age structure and regeneration of subalpine fir (*Abies fargesii)* forests across an altitudinal range in the Qinling Mountains, China. Forest Ecol Manag 259: 547-554. http://dx.doi.org/10.1016/j.foreco.2009.11.011

Darabant A, Rai PB, Tenzin K, Sangay T, and Gratzer G, 2007. Bamboo competition and favorable microsites determine recruitment of Tsuga dumosa seedlings at different spatial scales. RNR-RC Jakar, Bumthang, Bhutan.

De Chantal M, Leinonen K, Kuuluvainen T, Cescatti A, 2003. Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. For Ecol Manag 176(1-3): 321-336.

De Lima RAF, 2005. Gap size measurement: the proposal of a new field method. Forest Ecol Manag 214: 413-419. http://dx.doi.org/10.1016/j.foreco.2005.04.011

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol System 18: 431-451. http://dx.doi.org/10.1146/annurev.es.18.110187.002243

Ehrenfeld JG, 1980. Understory response to canopy gaps of varying size in a mature oak forests. Bulletin Torrey Botanical Club 107: 29-41. http://dx.doi.org/10.2307/2484848

Embaye K, Weih W, Ledin S, Christersson L, 2005. Biomass and nutrient distribution in highlands bamboo forest in southwest Ethiopia: implications for management. Forest Ecol Manag 204: 159-169. http://dx.doi.org/10.1016/j.foreco.2004.07.074

Gaudio N, Balandier P, Marquier A, 2008. Light-dependent development of two competitive species (*Rubus idaeus, Cytisus scoparius*) colonizing gaps in temperate forest. Ann For Sci 65: 104. http://dx.doi.org/10.1051/forest:2007076

Gonzalez ME, Veblen TT, Donoso C, Valeria L, 2002. Tree generation response in a lowland Nothofagus-dominated forest after bamboo die-back in south-central Chile. Plant Ecology 161: 59-73. http://dx.doi.org/10.1023/A:1020378822847

Griscom BW, Ashton MS, 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. Forest Ecol Manag 175: 445-454. http://dx.doi.org/10.1016/S0378-1127(02)00214-1

Gray A, Spies TA, 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78(8): 2458-2473. http://dx.doi.org/10.1890/0012-9658(1997)078[2458:MCOTSE]2.0.CO;2

Guo YX, Li G, Hu YN, Kang D, Wang DX, Yang GH, 2013. Regeneration of *Betula albosinensis* in Strip Clearcut and Uncut Forests of the Qinling Mountains in China. Plos one 8(3): e59375. http://dx.doi.org/10.1371/journal.pone.0059375

Harmon ME, Franklin JF, 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70: 48-59. http://dx.doi.org/10.2307/1938411

Holz A, Veblen TT, 2006. Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine Nothofagus forest in the southern Andes. J Veg Sci 17: 19-28. http://dx.doi.org/10.1658/1100-9233(2006)017[0019:tr-rtcm]2.0.co;2

Huenneke LF, 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. B Torrey Botanic Club 110: 170-175. http://dx.doi.org/10.2307/2996338

Kinny M, McElhinny C, Smith G, 2012. The effect of gap size on growth and species composition of 15-year-old regrowth in mixed blackbutt forests. Australian Forestry 75(1): 3-15. http://dx.doi.org/10.1080/00049158.2012.10676380

Kirchner K, Kathke S, Bruelheide H, 2011. The interaction of gap age and microsite for herb layer species in a near natural spruce forest. J Veg Sci 22: 85-95. http://dx.doi.org/10.1111/j.1654-1103.2010.01234.x

Larpkern P, Moe SR and Totland O, 2010. Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia 165: 161-168. http://dx.doi.org/10.1007/s00442-010-1707-0

Li J, Pei LY, Kang W, Zhao S, Yang HW, Li JQ, 2012. Study on Mosses Diversity in Wanglang National Nature Reserve, Sichuan Province. Acta Bot Boreali-Occidentalia Sinica 32(11): 2344-2351 [in Chinese with English abstract].

Li QZ, Bogaert J, Nijs I, 2005. Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation. Ecography 28: 777-790. http://dx.doi.org/10.1111/j.2005.0906-7590.04261.x

Liu Q, Hytteborn H, 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J Veg Sci 2: 391-402. http://dx.doi.org/10.2307/3235932

Liu Q, Wu Y, 2002. Effects of gap size on regeneration of subalpine coniferous forests in northwest Yunnan. Chin J Appl Environ Biol 8(5): 453-459 [in Chinese with English abstract].

Lusk CH, 2001. When is a gap not a gap? Light levels and leaf area index in bamboo-filled gaps in a Chilean rain forest. Gayana Bot. 58: 25-30. http://dx.doi.org/10.4067/S0717-66432001000100003

McGuire JP, Mitchell RJ, Moser EB, Pecot SD, Gjerstad DH, Hedman CW, 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can J For Res 31: 765-778. http://dx.doi.org/10.1139/x01-003

Montti L, Campanello PI, Gatti MG, Blundo C, Austin AT, Sala OE, Goldstein GH, 2011. Understory bamboo flowering provides a very narrow light window of opportunity for canopy-tree recruitment in a neotropical forest of Misiones, Argentina. Forest Ecol Manag 262: 1360-1369. http://dx.doi.org/10.1016/j.foreco.2011.06.029

Nakashizuka T, 1987. Regeneration dynamics of beech forests in Japan. Vegetatio 69: 169-175. http://dx.doi.org/10.1007/BF00038698

Nakashizuka T, 1988. Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). Ecol Res 3: 21-35. http://dx.doi.org/10.1007/BF02348692

Nakashizuka T, 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70: 1273-1278. http://dx.doi.org/10.2307/1938186

Nakashizuka T, Numata M, 1982a. Regeneration process of climax beech forest. I. Structure of beech forest with the undergrowth of Sasa. Jpn J Ecol 32: 57-67.

Nakashizuka T, Numata M, 1982b. Regeneration process of climax beech forest. II. Structure of beech forest under influence of grazing. Jpn J Ecol 32: 473-482.

Narukawa Y, Yamamoto S, 2001. Gap formation, microsite variation and the conifer seedling occurrence in a subalpine old-growth forest, central Japan. Ecol Res 16: 617-625. http://dx.doi.org/10.1046/j.1440-1703.2001.00424.x

Narukawa Y, Yamamoto S, 2002. Effects of coniferous and broad-leaved trees in a Japanese temperate mixed forest. J Veg Sci 2: 413-418.

Ostertag R, 1998. Belowground effects of canopy gaps in a tropical wet forest. Ecology 79(4): 1294-1304. http://dx.doi.org/10.1890/0012-9658(1998)079[1294:BEOCGI]2.0.CO;2

Pearson TRH, Burslem DFRP, Goeriz RE, Dalling JW, 2003. Interactions of gap size and herbivory on establishment, growth and survival of three species of Neotropical pioneer trees. J Ecol 91: 785-796. http://dx.doi.org/10.1046/j.1365-2745.2003.00803.x

Rao KS, Ramakrishnan PS, 1989. Role of bamboo in nutrient conservation during secondary succession following slash and burn agriculture (Jhum) in Northeast India. J Appl Ecol 26: 625-634. http://dx.doi.org/10.2307/2404087

Rousset O, Lepart J, 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). J Ecol 88: 401-412. http://dx.doi.org/10.1046/j.1365-2745.2000.00457.x

Runkle JR, 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62: 1041-1051. http://dx.doi.org/10.2307/1937003

Runkle JR, 1985. Disturbance regimes in temperate forests. The Ecology of Natural Disturbance and Patch Dynamics (Ed by S.T.A. Pickett and P.S. White), Academic Press, New York: 17-33.

Sapkota IP, Oden PC, 2009. Gap characteristics and their effects on regeneration, dominance and early growth of woody species. J Plant Ecol 2(1): 21-29. http://dx.doi.org/10.1093/jpe/rtp004

Schnitzer SA, Carson WP. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82: 913-919. http://dx.doi.org/10.1890/0012-9658(2001)082[0913:TGATMO]2.0.CO;2

Singh AN, Singh JS, 1999. Biomass, net primary production and impact of bamboo plantation on soil redevelopment in a dry tropical region. Forest Ecol Manag 119: 195-207. http://dx.doi.org/10.1016/S0378-1127(98)00523-4

Takahashi K, 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understory. J Veg Sci 8: 529-536. http://dx.doi.org/10.2307/3237203

Takahashi KS, Uemura S, Suzuki JI, Hara T, 2003. Effects of understory dwarf bamboo removal on soil water and the growth of overstory trees in a dense secondary Betula ermanii forest, northern Japan Ecol Res 18: 767-774. http://dx.doi.org/10.1007/s11284-003-0594-9

Takahashi L, 1994. Effect of size structure, forest floor type, and disturbance regime on tree species composition in a coniferous forest in Japan. J Ecol 82: 769-773. http://dx.doi.org/10.2307/2261442

Taylor AH, Jang SW, Zhao LJ, Liang CP, Miao CJ, Huang JY, 2006. Regeneration patterns and tree species coexistence in old-growth Abies-Picea forests in southwestern China. Forest Ecol Manag 223: 303-317. http://dx.doi.org/10.1016/j.foreco.2005.11.010

Taylor AH, Qin Z, 1988a. Regeneration patterns in old-growth Abies-Betula forests in the Wolong Natural Reserve, Sichuan, China J Ecol 76: 1204-1218. http://dx.doi.org/10.2307/2260643

Taylor AH, Qin Z, 1988b. Tree replacement patterns in subalpine Abies-Betula forests in Wolong Natural Reserve, China. Vegetation 78: 141-149. http://dx.doi.org/10.1007/BF00033423

Taylor AH, Qin Z, 1989. Structure and composition of selectively cut and uncut Abies-Tsuga forest in Wolong natural reserve and implications for panda conservation in China. Biol Conserv 47: 83-108. http://dx.doi.org/10.1016/0006-3207(89)90093-1

Taylor AH, Qin ZS, Jie L, 1996. Structure and dynamics of subalpine forests in the Wang Lang Natural Reserve, Sichuan, China. Plant Ecol 124: 25-38. http://dx.doi.org/10.1007/BF00045141

Tripathi SK, Sumida A, Shibata H, Uemura S, Ono K, Hara T, 2005. Growth and substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii* forest of northern Japan: effects of the removal of understory dwarf bamboo (*Sasa kurilensis*). Forest Ecol Manag 212: 278-290. http://dx.doi.org/10.1016/j.foreco.2005.03.030

Tsvuura Z, Griyths ME, Gunton RM, Franks PJ and Lawes MJ, 2010. Ecological filtering by a dominant herb selects for shade tolerance in the tree seedling community of coastal dune forest. Oecologia 164: 861-870. http://dx.doi.org/10.1007/s00442-010-1711-4

Veblen TT, 1982. Growth patterns of Chusquea bamboos in the understory of Chilean Nothofagus forests and their influences in forest dynamics. B Torr Bot Club 109: 474-487. http://dx.doi.org/10.2307/2996488

Veblen TT, 1989. Tree regeneration responses to gaps along a transandean gradient[J]. Ecology 70: 541-543. http://dx.doi.org/10.2307/1940197

Veblen TT, Donoso C, Schlegel FM, Escobar B, 1981. Forest dynamics in south-central Chile. J Biogeogr 8: 211-247. http://dx.doi.org/10.2307/2844678

Wang W, Franklin SB, Ren Y, Ouellette JR. 2006. Growth of bamboo *Fargesia qinlingensis* and regeneration of trees in a mixed hardwood-conifer forest in the Qinling Mountains, China. Forest Ecol Manag 234: 107-115. http://dx.doi.org/10.1016/j.foreco.2006.06.028

Wang YJ, Tao JP, Zhong ZC, 2009. Factors influencing the distribution and growth of dwarf bamboo, *Fargesia nitida,* in a subalpine forest in Wolong Nature Reserve, southwest China. Ecol Res 24(5): 1013-1021. http://dx.doi.org/10.1007/s11284-008-0573-2

Yamamoto S, 1993. Gap characteristics and gap regeneration in a subalpine coniferous forest on Mt. Ontake, central Honshu, Japan. Ecol Res 8: 277-285. http://dx.doi.org/10.1007/BF02347187

Yamamoto S, 1995. Gap characteristics and gap regeneration in subalpine old-growth coniferous forests, central Japan. Ecol Res 10: 31-39. http://dx.doi.org/10.1007/BF02347653

Zhang C, Zou CJ, Peltola H, Wang KY, Xu WD, 2013. The effects of gap size and age on natural regeneration of *Picea mongolica* in the semi-arid region of Northern China. New Forests 44: 297-310. http://dx.doi.org/10.1007/s11056-012-9318-8

Zhao ZJ, Eamus D, Yu Q, Li Y, Yang HW, Li JQ, 2012. Climate constraints on growth and recruitment patterns of Abies faxoniana over altitudinal gradients in the Wanglang Natural Reserve, eastern Tibetan Plateau. Aust J Bot 60: 602-614. http://dx.doi.org/10.1071/BT12051