Scientific Research and Essays Vol. 7(6), pp. 660-668, 16 February, 2012
Available online at http://www.academicjournals.org/SRE
DOI: 10.5897/SRE11.1100
ISSN 1992-2248 ©2012 Academic Journals

Full Length Research Paper

Effects of different bamboo densities on understory species diversity and trees regeneration in an *Abies faxoniana* forest, Southwest China

Yong-Jian Wang[1], Xue-Ping Shi[1] and Jian-Ping Tao [2]*

[1]College of Horticulture and Forestry Sciences of Huazhong Agricultural University, Wuhan, 430070, China.
[2]Key Laboratory of Eco-environments of Three Gorges Reservoir Region (Ministry of Education) of Southwest University, Chongqing 400715, China.

Accepted 23 December, 2011

Effects of dwarf bamboo, *Fargesia nitida*, on micro-environments, species diversity and regeneration on the floor were investigated at three conditions, high density (HB), low density (LB) and without *F. nitida* (UB) in a subalpine *Abies faxoniana* forest, southwest China. Relative photon flux density (RPFD) on the floor became unfavorable, and physical and chemical features of soil improved with the density of *F. nitida*. Thickness of litters increased and bryophytes decreased with the density of *F. nitida*. Dominance of *A. faxoniana* in shrub layer, understory species diversity and trees regeneration were lowest in HB, however, which showed little significant differences in UB and LB. RPFD under bamboo layer and surface soil conditions (thickness of litters and bryophytes etc.) resulting from different bamboo density were significantly correlated with understory species diversity and *A. faxoniana* regeneration. High density of bamboo has a fatal influence on understory species diversity and tree regeneration. However, there is not a significantly negative effect of low density bamboo (< 10 culms/m^2) in our study. Therefore, dynamics of bamboo density (flowering or by gap disturbance etc.) can provide useful guidelines for understanding understory species dynamics and regeneration of subalpine forest in this region.

Key words: *Fargesia nitida*, dwarf bamboo, micro-environments, tree regeneration, understory species diversity.

INTRODUCTION

Dwarf bamboos were recognized as determinant to the structure and dynamics of Chinese forests (Taylor et al., 2004; Wang et al., 2009) and Japanese forests (Noguchi and Yoshida, 2005; Itô and Hino, 2007) for their wide distribution and exclusive density. Many studies have reported the negative effects of dwarf bamboo. The distribution and dominance of dwarf bamboo, *Sasa* and *Fargesia* spp., impeded the surviving and regeneration of tree seeds (Iida, 2004), seedlings and saplings (Nakagawa and Kurahashi, 2005; Li et al., 2007a, b; Larpkern et al., 2011) and mature trees (Takahashi et al., 2003), decreased understory plant species diversity (Noguchi and Yoshida, 2005) and the availability of microbial biomass C and N (Tripathi et al., 2006a) in soil. However, most previous studies have investigated the understory species diversity and responses of tree seedlings to the presence or absence of understory plants, rather than developing quantitative classification of understory plants to analyze the effect of different bamboo densities or coverage. In forest understory, radiation intensity and other microclimatic factors played a

*Corresponding author. E-mail: wangyj@mail.hzau.edu.cn, taojp@swu.edu.cn. Tel/Fax: +86-27-87282010.

Abbreviations: HB, high density of *F. nitida*; **LB,** low density of *F. nitida*; **UB,** without *F. nitida*; **PPFD,** photosynthetic photon flux density; **RPFD,** relative photon flux density.

major role in the growth, survival and regeneration of understory species (Emborg, 1998; Messier et al., 1998). Many studies indicated the intense change of the light and other microclimatic factors on the floor with the abundance of understory shrub was significant for diverse species, the new and advanced regeneration in different forests (Taylor et al., 2004; Montti et al., 2011). Therefore, it is a key to discussing the influence of variation in forest floor conditions with abundance of dwarf bamboo, on understory species diversity and tree regeneration.

Dwarf bamboo, *Fargesia nitida*, being one of the main foods for the giant panda (*Ailuropoda melanoleuca* David) is widespread in the subalpine forest of Wolong Nature Reserve, southwest China. Patch distribution of different bamboo densities was obvious in *Abies faxoniana* forest of this region due to natural disturbance such as fall and broken branches of trees (Wang et al., 2009). 1 to 10 and > 25 culms/m^2 class of bamboo density took more than 30%, respectively. Our previous studies showed that existence of *F. nitida* had significant negatively influence on understory species diversity and on establishment of *A. faxoniana* seedlings (Wang et al., 2007b; Li et al., 2007b). Different bamboo densities might influence on growth and survival of tree seedlings (Taylor et al., 2004). However, we have not previously documented the effects of different bamboo densities on micro-environments, species diversity and regeneration on the floor, and the relationship between bamboo characteristics and understory species diversity and regeneration of *A. faxoniana*. In subalpine forest of southwest China, smooth tree regeneration will require the control of dwarf bamboo understory. From this perspective, this study will provide basis on the quantitative relationships between the density of dwarf bamboo and understory species diversity and trees regeneration (Itô and Hino, 2007).

In this study, our objectives are to understand the effects of three dominant *F. nitida* densities (high density, low density and without bamboo) on the floor in subalpine *A. faxoniana* forest of this region and specifically to discuss the following questions: 1) Effects of different bamboo densities on understory species composition and diversity; 2) Effects of different bamboo densities on floor conditions and trees regeneration; 3) The relationship between floor characteristics (including bamboo characteristics) and understory species diversity and regeneration of *A. faxoniana*.

MATERIALS AND METHODS

Study area

The study site was located in subalpine dark coniferous forest near the Wolong Subalpine Dark Coniferous Forest Ecosystem Research Station (102°58'21'' E, 30°51'41'' N, 2 800 m a. s. l.) in the southwest of Wolong Nature Reserve, Sichuan Province, China. The climate is warm and the annual mean temperature is 4.3°C, and the annual precipitation and annual evaporation capacity are about 848.9 and 772.5 mm, respectively. The annual sunshine duration lasts approximately 1185.4 h (Yu et al., 2006). The compositions of vegetation are abundant and vegetation layers are distinct. Two sub-layers occur in tree layer, I sub-layer: 30 to 40 m, *A. faxoniana* is constructive species; II sub-layer: 10 to 20 m, *A. faxoniana*, *Betula utilis*, *Betula albo-sinensis* and *Acer caudatum* var. *prattii* are the dominant species. Shrub layer: 1 to 7 m, bamboo *F. nitida* is the dominant species, and companion species include *Rhododendron* spp., *Smilax* spp., *Lonicera* spp., *Viburnum betulifolium*, *Sorbus rufopilosa*, etc. Species of herb layer distribute heterogeneously and the coverage varies from 10 to 70%, *Cacalia* spp., *Elatostema obtusum* and *Carex* sp. are dominant species. The main tree seedlings regenerating on the floor are *A. faxoniana*, *B. utilis* and *A. caudatum* var. *prattii* (Wang et al., 2009).

F. nitida (Mitford) Keng f. is a dwarf bamboo and a food source for the giant panda. It is a perennial but monocarpic woody clonal plant with a 50 to 60 years flowering periodicity. The culms, 2 to 5 m in height and 1 to 2 cm in width form a fasciculate ramet group or a scattered ramet distribution. The clonal growth of *F. nitida* depends on rhizomatous expansion, actually belonging to phalanx type. The plant is distributed in southern Gansu and southwest Sichuan province, China (Yu et al., 2006).

Community inventories

Measurement of community was mainly conducted in *A. faxoniana* forest in mid-summer (August 2006) when the vegetation was mostly developed and the annual growth of *F. nitida* reached the stable stage. We chose three dominant conditions of bamboo density: high density of *F. nitida* (HB), low density of *F. nitida* (LB) and without *F. nitida* (UB) respectively in coniferous forest (Table 1), according to: HB— average bamboo density > 25 culms/m^2 and bamboo coverage 50 to 85%; LB— 1 culm/m^2 ≤ average bamboo density ≤ 10 culms/m^2, and bamboo coverage 2 to 20%; UB— the distribution of *F. nitida* is dispersed, average bamboo density < 1 culm/m^2 and bamboo coverage < 2%. Six 10 × 20 m plots per bamboo density condition (study site) were installed. The distance between two study sites and two plots in the same bamboo condition was more than 500 and 30 m, respectively. Topography factor and litters features were recorded and canopy gap was measured by the LAI-2000 plant canopy analyzer (LI-COR, Lincoln, USA) in each plot. Each 10 × 20 m plot was composed of eight 5 × 5 m quadrats in which the height, diameter at breast, crown of each tree and height, coverage of each shrub, and overstory coverage, shrub coverage, herb coverage, density and coverage of *F. nitida* were measured. Five 1 × 1 m small quadrat was set up in each 5 × 5 quadrat (totally forty 1 × 1 m small quadrats in each plot) by quincunx sampling, and average height and coverage of each herb species were measured in each 1 × 1 m small quadrat. Environmental factors were measured at each plot.

Photosynthetic photon flux density (PPFD) was measured at 0.5 m height above the ground in the center of each plot by LI-COR LI-191SA line quantum sensors (LI-COR, Lincoln, USA) and recorded by LI-1400 data loggers (LI-COR, Lincoln, USA). Relative photon flux density (RPFD) was measured simultaneously under the canopies and at open sites respectively on overcast day by the same sensors. The measurements were conducted on several clear days in July 2006 (mid-summer, leafy season). Due to the rapid change in light intensity, the average of the 60 records in 1 min at the same time (1:00 pm) was taken as the value.

Regeneration inventories

In view of basic knowledge about the growth of *A. faxoniana* and *B. utilis* and class distribution in the previous study (Li et al., 2007b), class sizes of these two tree species were divided into the following four classes in each plot: saplings, height (H) ≥ 0.33 m, diameter at

Table 1. General conditions of three stands with different densities of *Fargesia nitida*.

Plots	Elevation (m)	Slope (°)	Bamboo density (culms/m^2)	Canopy coverage (%)	RPFD under canopy (%)
HB	2730-2740	18-30	>25	83.32±2.15	8.51±0.55
LB	2750-2760	15-25	1-10	84.59±1.87	8.32±0.37
UB	2750-2765	9-25	<1	82.73±1.94	8.36±0.58

HB: high density of *F. nitida* condition; LB: low density of *F. nitida* condition; UB: without *F. nitida* condition.

Table 2. Characteristics of three stands with different densities of *Fargesia nitida* (Mean±SE).

Community characteristics	Density of *Fargesia nitida*		
	HB	LB	UB
Thickness of litters (cm)	2.70±0.27^a	0.81±0.19^b	0.36±0.11^b
Thickness of bryophytes (cm)	1.38±0.24^c	3.76±0.25^b	5.00±0.35^a
Thickness of soil humus (cm)	11.60±0.33^a	6.30±1.25^b	7.6±1.43^b
Bamboo density (culms/m^2)	38.3±1.9^a	7.0±0.4^b	0.8±0.1^c
Bamboo coverage (%)	82.56±4.75^a	16.79±1.37^b	1.26±0.12^c
Coverage of herb (%)	10.70±1.09^b	47.13±2.45^a	40.58±3.42^a
RPFD under bamboo layer (%)	0.91±0.04^c	6.12±0.42^b	8.24±0.28^a

Different letters indicate significant differences at P < 0.05 level between three conditions.

breast height (DBH) < 2.5 cm; small trees: 2.5 cm ≤ DBH < 7.5 cm; middle trees: 7.5 cm ≤ DBH < 22.5 cm. Height and DBH of small trees and middle trees, height and basal diameter of saplings and were measured in six 10 × 20 m plots per bamboo density condition. The number of seedlings (H < 0.33 m) were investigated in 1 × 1 m the small quadrat for herb investigation above and total area in each plot was 40 m^2.

Soil sampling and analysis

A mixed soil sample was from three typical points (with average bamboo density and undisturbed condition) of each plot, and soil was got in the following two layers (0 to 15 cm and 15 to 30 cm depth) for physical and chemical analysis. Physical features of soil including water content (drying at 105°C for 48 h), unit weight of soil (using method of cutting ring), total porosity and capillary porosity were measured in Wolong Research Station. Chemical feature of soil were measured in our laboratory after taking them back and air drying. Total nitrogen (N) was determined by Kjeldahl Distillation System B-324 (BUCHI, Switzerland) by digestion with oil of vitrio, $CuSO_4$-K_2SO_4 mixture as catalyst. Total phosphorus (P) was analyzed using the molybdate blue method after digestion with sulfuric acid and perchloric acid.

Data analysis

1) The important values (IV) of species were calculated using the following formulas (Wang et al., 2006): IV shrub and herb layer = (relative height + relative coverage + relative frequency) × 100/3.

2) Species diversity indices: Shannon-Wiener index $H = -P_i \ln P_i$; Simpson index $D = 1 - \sum P_i^{\ 2}$; Pielou evenness index $J = (-\sum P_i \ln P_i) / \ln S$; Richness index *S*. P_i is the relative IV of the species and *S* is the total number of species (Kanieski et al., 2010).

3) Parameters analysis: figures were drawn by OriginPro 7.0 and all statistical analyses were carried out using SPSS (SPSS 11 Copyright: SPSS Inc.). We used one-way ANOVA to test for effects of different bamboo conditions (high density of *F. nitida*, low density of *F. nitida* and without *F. nitida*) on species diversity of shrub and herb layer, dominant trees regeneration and physical and chemical features of soil and a multiple comparison test was used to determine significant differences among three treatments. Correlation analysis (Spearman coefficient) was used to analyze the relationship between floor characteristics (including bamboo characteristics) and understory species diversity and regeneration of *A. faxoniana*.

RESULTS

Effects on understory conditions

There were no significant differences in canopy coverage and RPFD under canopy of three bamboo conditions (Table 1). Coverage of shrub increased, and coverage of herb and RPFD on the floor decreased with the density of *F. nitida*. Thickness of litters and soil humus in high density of *F. nitida* condition (HB) was higher than other two conditions. Thickness of bryophytes decreased with the density of *F. nitida* (Table 2). The soil physical features were shown in Table 3. For each layer, water content and total porosity increased and unit weight of soil decreased with the density of *F. nitida*. There were no significant differences in capillary porosity in first layer between three bamboo conditions. Capillary porosity in low density *F. nitida* condition (LB) and HB was higher than that in without

Table 3. The soil physical and chemical features of three stands with different densities of *Fargesia nitida* (Mean±SE).

Soil depth	Bamboo density	Physical characteristics				Chemical characteristics	
		Water content (%)	Unit weight (g·cm^{-3})	Total porosity (%)	Capillary porosity (%)	Total N (g· Kg^{-1})	Total P (g· Kg^{-1})
First layer (0-15 cm)	HB	69.22±2.56^{a}	0.714±0.014^{c}	71.02±0.48^{a}	52.36±1.91	2.14±0.24^{a}	0.70±0.03^{a}
	LB	60.96±2.75^{b}	0.853±0.014^{b}	67.68±0.66^{b}	51.96±1.99	1.36±0.44^{ab}	0.60±0.03^{a}
	UB	58.08±3.25^{b}	0.900±0.009^{a}	62.77±0.78^{c}	56.53±2.83	1.08±0.03^{b}	0.46±0.05^{b}
Second layer (15-30 cm)	HB	57.97±4.12^{a}	0.881±0.018^{c}	65.26±0.69^{a}	55.27±4.55a	0.73±0.13	0.42±0.03
	LB	53.79±3.89^{a}	1.030±0.024^{b}	61.01±0.89^{b}	59.24±1.57a	0.61±0.15	0.35±0.03
	UB	40.10±0.73^{b}	1.123±0.019^{a}	57.11±0.28^{c}	44.64±0.25b	0.71±0.20	0.35±0.01

Different letters indicate significant differences at P < 0.05 level between three conditions.

bamboo condition (UB) in second layers (Table 3). The total N and P of first layer of soil were higher under high density of *F. nitida*, but there were no significant differences between two parameters between LB and HB.

Effects on understory species diversity

The species composition for each condition was illustrated in Table 4. In shrub layer, the dominant species was *F. nitida*, and main companion species included *A. faxoniana* and *V. betulifolium*, etc in HB. The dominant species were *A. faxoniana* and *Rhododendron* spp., and main companion species also were similar in both LB and UB such as *Hydrangea xanthoneura* and *V. betulifolium*. In herb layer, *Carex* sp. dominated in HB. Dominant species in LB were *Cacalia otopteryx* and *Ctenitis* sp. *Cacalia* spp. *C. otopteryx*, *C. palmatisecta* and *C. deltophylla* dominated in UB. *Cacalia* genus gradually dominated on the floor with the decrease in bamboo density, and the differences in herb composition were distinct between HB and UB. In shrub layer, all indices in HB were lower than those in LB and UB, and all indices were not significantly different in LB versus UB. In herb layer, all indices almost were lower in HB than in LB and UB except that evenness had no significant differences among three conditions. There were no significant differences in all indices between LB and UB (Figure 2).

Effects on trees regeneration

Regeneration inventories of seedlings indicated that *B. utilis*, *A. faxoniana* and total amounts in LB and UB were higher than those in HB and *B. utilis* amounts in LB were slightly higher than those in UB (Figure 3). Saplings, small trees and middle trees of *B. utilis* occurred at an average density not significantly different among three conditions. The average density of saplings of *A. faxoniana* showed gradually significant increase with the decrease in bamboo density, and small trees and middle trees had significantly higher densities in LB and UB than those in HB (Figure 3).

The relationship between floor characteristics and understory species diversity and regeneration

Understory woody diversity (H and S), herbaceous diversity (H and S) were all significantly positively correlated with RPFD under bamboo layer and thickness of bryophytes, and significantly negatively correlated with bamboo density, bamboo coverage and thickness of humus. Thickness of litters had significant negative influence on understory herbaceous diversity (Appendix A). *A. faxoniana* regeneration (from seedling to middle trees) were all significantly positively correlated with RPFD under bamboo layer and thickness of bryophytes, and significantly negatively correlated with bamboo density and thickness of litters. Bamboo coverage had significant negative influence on regeneration except for middle trees. Canopy coverage and understory RPFD had no significant correlation

Table 4. Main species and their importance value in stands with different densities of *Fargesia nitida* (total 1200 m^2). Species (IV>5) in shrub and herb layer were listed in the previous table.

No.	Species	Importance values		
		HB	LB	UB
Shrub layer (including saplings and seedlings of tree species)				
1	*Fargesia nitida*	49.43	8.27	
2	*Abies faxoniana*	8.61	16.97	14.68
3	*Viburnum betulifolium*	5.38	6.78	11.07
4	*Rhododendron Calophytum*		9.00	5.65
5	*Rhododendron fictolacteum*		11.13	13.86
6	*Hydrangea xanthoneura*		10.36	6.04
7	*Lonicera tangutica*		5.66	
8	*Rosa sikangensis*			5.87
Herb layer				
1	*Carex* sp.	17.78	5.36	5.56
2	*Cacalia profundorum*	12.03	9.05	
3	*Elatostema obtusum*	9.27	8.34	
4	*Streptopus* sp.	8.36		
5	*Saxifraga stolonifera*	7.76		
6	*Cystopteris montana*	6.20	6.68	7.53
7	*Cacalia otopteryx*		12.42	8.03
8	*Cacalia palmatisecta*		10.27	9.57
9	*Cacalia deltophylla*			11.20
10	*Cacalia tangutica*			5.07
11	*Ctenitis* sp.		12.89	
12	*Allium ovalifolium*		6.22	

with understory species diversity and regeneration (Appendix A). Regression also showed that understory woody richness and regeneration of *A. faxoniana* saplings were significantly positively correlated with RPFD under bamboo layer from change of bamboo density. Herb richness was higher correlated with thickness of litters (Figure 1).

DISCUSSION

Under homogeneous canopy of a subalpine *A. faxoniana* forest in this region, dwarf bamboo, *F. nitida* had significant effect on understory micro-environment. Coverage of herb and thickness of bryophytes decreased with the bamboo density due to strong decrease of RPFD under bamboo layer, the same results were observed by Emborg (1998) and Wang et al. (2007b). Widespread dwarf bamboo had large amount of litter fall through the huge gross primary production (Tripathi et al., 2006b; Sakai et al., 2006) which leads lots of litters and humus on the forest floor. The decrease of RPFD under bamboo layer might also influence decomposition of litters and forming of humus (Li et al., 2006). These further increased total N and P of surface soil (Wu et al., 2009). Widespread dwarf bamboo increased water content, total porosity and capillary porosity and decreased unit weight of soil through the activities of fine-root system and anfractuosity of rhizomes in soil (Fukuzawa et al., 2007). Thus, in *A. faxoniana* pure forest with exclusive distribution of dwarf bamboo, air temperature and relative moisture might change with RPFD under bamboo layer (Campanello et al., 2007; Montti et al., 2011); and surface soil features (thickness of bryophytes, litters and soil humus) also dramatically changed. These variations in micro-environment under bamboo layer might lead to the change of species distribution patterns within *A. faxoniana* pure forest.

Results from the comparisons of species diversity and correlation analysis showed that bamboo characteristics were significantly related to understory species diversity. The dense *F. nitida* (HB) had significantly negative effect on dominance of *A. faxoniana* and *Rhododendron* species in shrub layer and *Cacalia* species in herb layer and on species diversity of both layers. Due to high bamboo coverage in shrub layer, there was low RPFD (< 1%) for species on the floor as dense *F. nitida* limited speices diversity and regeneration of *A. faxoniana* saplings (Figure 1). Some studies found that most species developed poorly and could be limited at RPFD < 3%

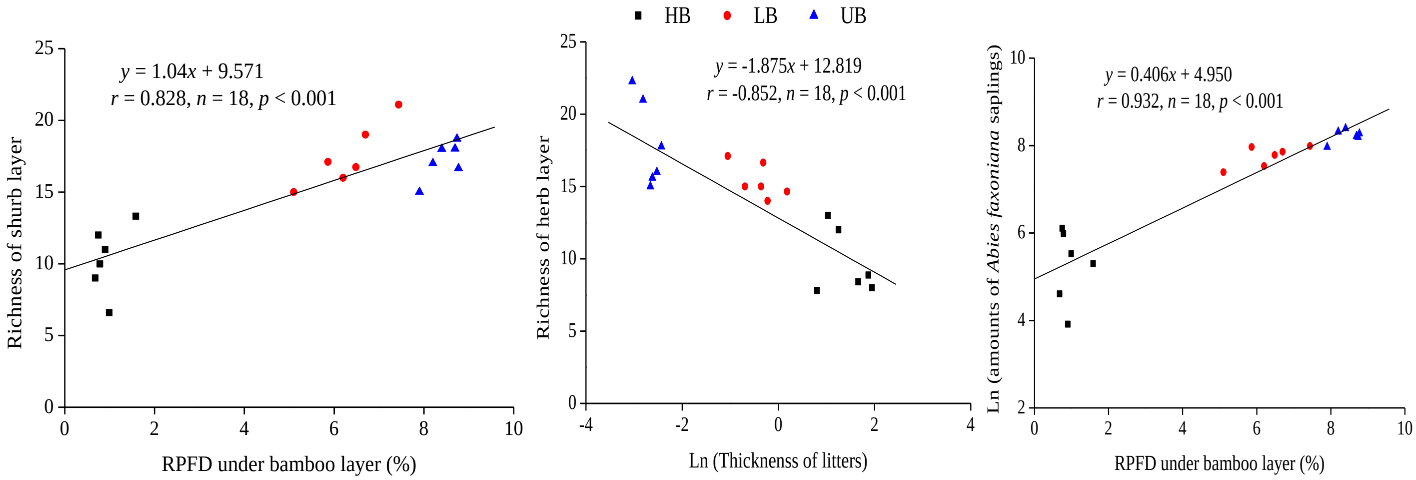

Figure 1. Regression analysis between influencing factors (RPFD under bamboo layer and thickness of litters) and understory species richness and regeneration in Abies faxoniana pure forest. P value and r are shown for each model.

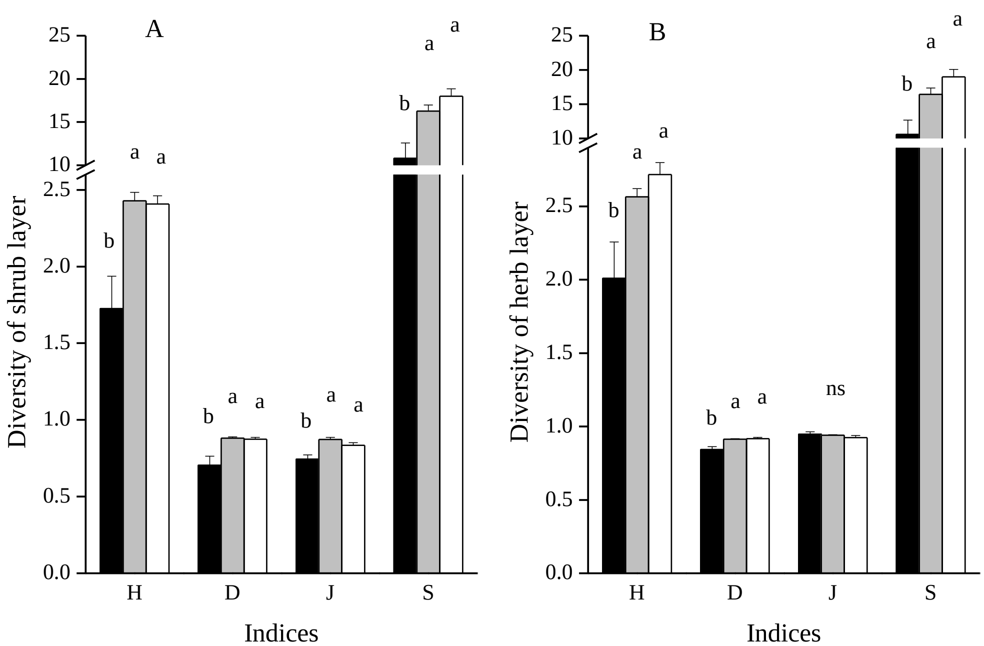

Figure 2. Understory species diversity in three *Fargesia nitida* conditions of subalpine *Abies faxoniana* forest, southwest China. Species diversity indices of shrub layer (A) and species diversity indices of herb layer (B).HB: high density of *F. nitida* condition; LB: low density of *F. nitida* condition; UB: without *F. nitida* condition. Letters (a, b) quantitatively indicate significantly differences (P<0.05). H: Shannon-Wiener diversity index; D: Simpson diversity index; J: Evenness index and S: Richness index.

(Emborg, 1998). Dense culms and rhizomes anfractuosity of *F. nitida* invaded and occupied the above/underground growth space which leads other shrubs and herbs have no space to live (Wang et al., 2007b). Thick litters of *F. nitida* in surface soil might restrict regeneration and survival of herbs through correlation analysis. The low RPFD, thick litters, dense culms and anfractuosity of their rhizomes in dense *F. nitida* condition which restrict the dominant and survival of species (including light-demanding species of *Cacalia* spp.), and just good

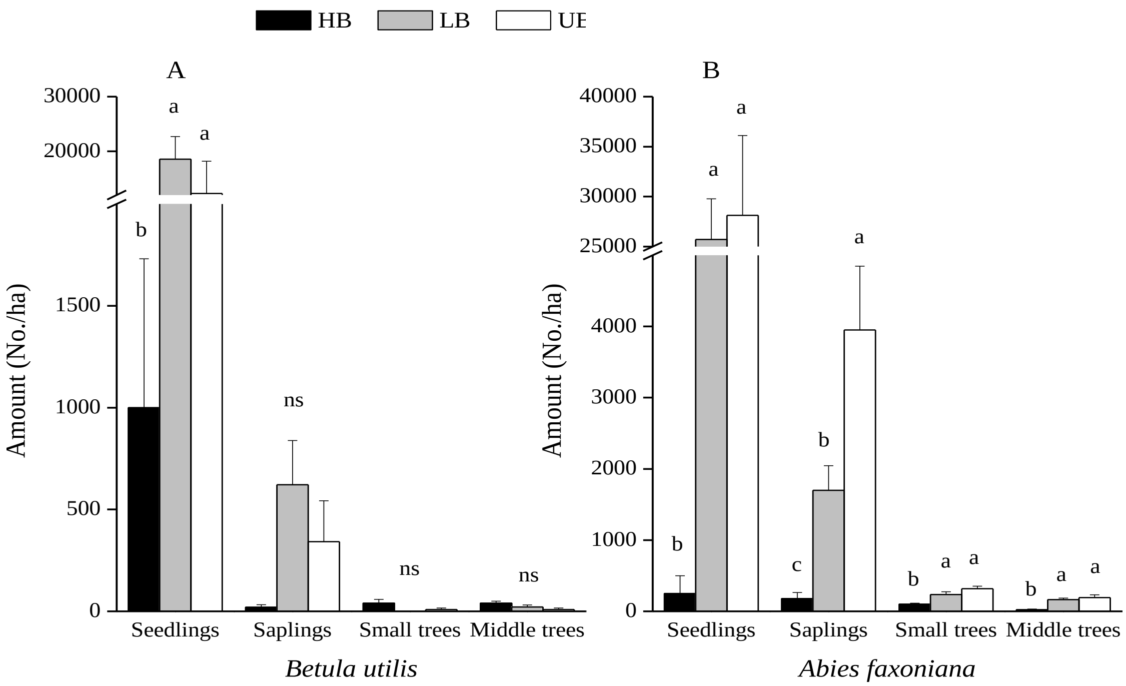

Figure 3. Class sizes of *Betula utilis* and *Abies faxoniana* in three *Fargesia nitida* densities of subalpine dark coniferous forest, southwest China. Class sizes of *Betula utilis* (A) and class sizes of *Abies faxoniana* (B).

for some extremely shade-tolerant species, *Elatostema obtusum* and *Saxifraga stolonifera* in the floor. However, in low density of *F. nitida* condition (LB), we did not find obvious negative effect on species composition and diversity.

RPFD under bamboo layer (about 6.1%) in LB was helpful to both extremely shade-tolerant and other species especially for herbs (Emborg, 1998). Thin litters might be helpful to seeds germination, growth of plants and propagation of many species and thick bryophytes reflected strong water retaining capacity for growth of plants (Li et al., 2006). As high bamboo condition, low bamboo condition could provide a protected layer to species survival on the floor away from broken branches of *A. faxoniana*. Results from tree regeneration, regression and correlation analysis also showed that bamboo characteristics were significantly related to understory trees regeneration. Regenerations of *B. utilis* were failure do not matter in bamboo or without bamboo condition due to the characteristics of pioneer tree species. The demand for light in *Abies* genus (*A. alba*) increased with the age. Trees of 1 to 2 and 5 years required 1.7 to 2.7 and 5% RPFD respectively (Robakowski et al., 2003; Lin and Liu, 2008). Thus, the dense *F. nitida* had significantly negative influence on tree regeneration (from seedlings to middle trees of *A. faxoniana* due to low light and other floor conditions (Nakagawa and Kurahashi, 2005; Li et al., 2007a, b; Wang et al., 2007a; Larpkern et al., 2011). However, we did not found obvious negative effect on tree regeneration at low bamboo density. There were no significant differences in floor conditions between LB and UB except for several soil parameters.

RPFD under bamboo layer (> 6%) was helpful to seedlings regeneration (Robakowski et al., 2003; Lin and Liu, 2008). Thin litters and thick bryophytes (reflected strong combination of light-water) in surface soil might be helpful to seeds germination and growth of tree seedlings (Li et al., 2006). LB could provide a protected layer to *A. faxoniana* survival on the floor away from broken branches of canopy.

Conclusions

High density of bamboo has a fatal influence on understory species diversity and tree regeneration. However, there is no significant negative effect of low density bamboo in our study. Different densities of dwarf bamboo might have distinguished effects on understory species diversity and tree regeneration. Bamboo density plays a significant role in maintenance of species diversity and tree regeneration on the floor. We suggest fine-scale relationship between the abundance of dwarf bamboo and understory species diversity should be addressed further to understand their quantitative relationships.

Further studies on dynamic of bamboo density (such as flowering or canopy disturbance) can be helpful to understanding understory environmental changes, and species dynamics and regeneration of *A. faxoniana* forest in this region.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (No. 31000194, 31070404) and by the Fundamental Research Funds for the Central Universities (2009BQ067). The authors are grateful to Chao-Long Yan, Yuan Li, Xiao-Hong Yu, Yi Xi and Qin Liang for their valuable assistance.

REFERENCES

Campanello PI, Gatti MG, Ares A, Montti L, Goldstein G (2007). Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. Forest Ecol. Manage., 252: 108-117.

Emborg J (1998). Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecol. Manage., 106: 83-95.

Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa K (2007). Vertical distribution and seasonal pattern of fine-root dynamics in a cool–temperate forest in northern Japan: implication of the understory vegetation, *Sasa* dwarf bamboo. Ecol. Res., 22: 485-495.

Holz CA, 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.

Iida S (2004). Indirect negative influence of dwarf bamboo on survival of *Quercus* acorn by hoarding behavior of wood mice. Forest Ecol. Manag. 202: 257-263.

Itô H, Hino T (2007). Dwarf bamboo as an ecological filter for forest regeneration. Ecol. Res., 22: 706-711.

Kanieski MR, Araujo BAC, Longhi SJ (2010). Diversity quantification in mixed *Ombrophilous* forest by different alpha indexes. Scientia Forestalis, 38: 567-577.

Larpkern P, Moe SR, Totland Ø (2011). Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia, 165: 161-168.

Li FX, Wang YF, Zhan QF, Xu B, Zhai DC, Dang GD (2006). Species diversity of floor bryophyte communities in Foping Nature Reserve. Chin. J. Plant. Ecl., 30: 919-923.

Li Y, Tao JP, Wang YJ, Yu XH, Xi Y (2007a). Effects of *Fargesia nitida* on regeneration of *Abies faxoniana* seedlings near the edge of subalpine dark coniferous forest. Chin. J. Plant Ecol., 31: 283–290.

Li Y, Tao JP, Wang YJ, Yu XH, Xi Y (2007b). Effects of *Fargesia nitida* on the population dynamics of *Abies faxoniana* at initial stage in dark coniferous forest. Acta Ecol. Sin., 27: 1041-1049.

Lin B, Liu Q (2008) Plasticity responses of 4 tree species in subalpine-coniferous-forest to different light regimes. Acta Ecol. Sin., 28: 4665-4675.

Messier C, Parent S, Bergeron Y (1998). Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci., 9: 511-520.

Montti L, Campanello PI, Gatti MG, Blundo C, Austin AT, Sala OE, Goldstein G (2011). Understory bamboo flowering provides a very narrow light window of opportunity for canopy tree recruitment in a neotropical forest of Misiones, Argentina. 2011. Forest Ecol. Manage., 262: 1360-1369.

Nakagawa M, Kurahashi A (2005). Factors affecting soil-based natural regeneration of *Abies sachalinensis* following timber harvesting in a sub-boreal forest in Japan. New For., 29: 199-205.

Noguchi M, Yoshida T (2005). Factors influencing the distribution of two co-occurring dwarf bamboo species (*Sasa kurilensis* and *S. senanensis*) in a conifer-broadleaved mixed stand in northern Hokkaido. Ecol. Res., 20: 25-30.

Robakowski P, Montpied P, Dreyer E (2003). Plasticity of morphological and physiological traits in response to different levels of irradiance in seedlings of silver fir (*Abies alba* Mill). Trees, 17: 431-441.

Sakai T, Akiyama T, Saigusa N, Yamamoto S, Yasuoka Y (2006). The contribution of gross primary production of understory dwarf bamboo, *Sasa senanensis*, in a cool-temperate deciduous broadleaved forest in central Japan. Forest Ecol. Manage., 236: 259-267.

Takahashi K, Uemura S, Suzuki J, Hara T (2003). Effects of understory dwarf bamboo on soil water and the growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan. Ecol. Res. 18: 767-774.

Taylor AH, Huang JY, Zhou SQ (2004). Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies–Betula* forests in southwestern China: a 12-year study. Forest Ecol. Manage., 200: 347-360.

Tripathi SK, Sumida A, Ono K, Shibata H, Uemura S, Takahashi K (2006a). The effects of understorey dwarf bamboo (*Sasa kurilensis*) removal on soil fertility in a *Betula ermanii* forest of northern Japan. Ecol. Res., 21: 315-320.

Tripathi SK, Sumida A, Shibata H, Ono K, Uemura S, Kodama Y, Hara T (2006b). Leaf litterfall and decomposition of different above- and belowground parts of birch (*Betula ermanii*) trees and dwarf bamboo (*Sasa kurilensis*) shrubs in a young secondary forest in Northern Japan. Biol. Fertil. Soils, 43: 237-246.

Wang W, Franklin SB, Cirtain MC (2007a). Seed germination and seedling growth in the arrow bamboo *Fargesia qinlingensis*. Ecol. Res., 22: 467-474.

Wang YJ, Tao JP, Li Y, Yu XH, Xi Y (2007b). Effects of *Fargesia nitida* on species diversity and trees regeneration in different forest cycles of subalpine forest in Wolong Nature Reserve. Sci. Silvae Sin., 43(2): 1-7.

Wang YJ, Tao JP, Zhang WY, Zang RG, Ding Y, Li Y, Wang W (2006). Vegetation restoration patterns and their relationships with disturbance on the Giant Panda Corridor of Tudiling, Southwest China. Acta Ecol. Sin. Int. J., 26: 3525-3532.

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: 1013-1021.

Wu FZ, Yang WQ, Wang KY, Wu N, Lu YJ (2009). Effect of stem density on leaf nutrient dynamics and nutrient use efficiency of dwarf bamboo. Pedosphere, 19: 496-504.

Yu XH, Tao JP, Li Y, Wang YJ, Xi Y, Zhang WY, Zang RG (2006). Ramet population structure of *Fargesia nitida* (Mitford) Keng f. et Yi in different successional stands of the subalpine coniferous forest in Wolong Nature Reserve. J. Integr. Plant Biol., 48: 1147-1153.

Appendix A

Table 1. Correlation analysis between understory habitat characteristics, and understory species diversity and *Abies faxoniana* regeneration. *:p<0.05; **:p<0.01.

Parameter types	Parameters	Understory habitat characteristics							
		Canopy coverage	Understory RPFD	RPFD under bamboo layer	Bamboo density	Bamboo coverage	Thickness of litters	Thickness of bryophytes	Thickness of humus
Woody diversity	*H*	0.383	-0.571	0.750(*)	-0.683(*)	-0.674(*)	-0.617	0.728(*)	-0.695(*)
	S	0.188	-0.468	0.828(**)	-0.678(*)	-0.728(*)	-0.594	0.739(*)	-0.714(*)
Herbaceous diversity	*H*	0.289	0.034	0.750(*)	-0.767(*)	-0.700(*)	-0.683(*)	0.628	-0.787(*)
	S	0.200	-0.056	0.817(**)	-0.766(*)	-0.741(*)	-0.724(*)	0.710(*)	-0.765(*)
Abies faxoniana	Seedlings	0.256	-0.173	0.929(**)	-0.912(**)	-0.929(**)	-0.879(**)	0.798(**)	-0.496
Regeneration	Saplings	0.358	-0.101	0.867(**)	-0.917(**)	-0.833(**)	-0.883(**)	0.753(*)	-0.653
	Small trees	0.216	-0.306	0.928(**)	-0.810(**)	-0.793(*)	-0.827(**)	0.839(**)	-0.712(*)
	Middle trees	0.026	0.056	0.672(*)	-0.724(*)	-0.655	-0.877(**)	0.786(*)	-0.624