Sains Malaysiana 41(6)(2012): 649–657

Effects of Fine-Scale Pattern of Dwarf Bamboo on Understory Species Diversity in *Abies faxoniana* Forest, Southwest, China

(Kesan Skala-Halus Buluh Kerdil Terhadap Kepelbagaian Spesies Bawahan
di Hutan *Abies faxoniana*, Barat Daya China)

YONG-JIAN WANG, XUE-PING SHI, YUE PENG, ZHANG-CHENG ZHONG & JIAN-PING TAO*

ABSTRACT

Dwarf bamboo is recognized as a significant determinant of the structure and dynamics in temperate forests. Quantitative relationships between the abundance (density and coverage) of dwarf bamboo, Fargesia nitida*, and micro-environments, species diversity on the floor were estimated in an* Abies faxoniana *pure forest in southwest China. Understory micro-environmental conditions (daily differences temperature and moisture, RPPFD under bamboo layer and ground cover) changed dramatically with the bamboo density. Stepwise multiple regression analyses indicated that abundance of* F. nitida *was mainly correlated with canopy characteristics and disturbance factors in the* A. faxoniana *pure forest. All richness indices decreased significantly with the bamboo density and RPPFD under bamboo layer. Importance values (IV) of understory species in different bamboo densities and Detrended canonical correspondence analysis (DCCA) indicated three understory plant groups, resistant to high bamboo abundance (Group A), resistant to intermediate bamboo abundance (Group B) and sensitive to bamboo abundance (Group C). These groups mainly responded to abundance of bamboo and RPPFD under bamboo layer, resulted from the integration of characteristics of bamboo, canopy and topography factors. Different bamboo abundance had different influences on understory species diversity and groups. Dense* F. nitida *condition (> 10 culms/m^2) had significant negative effect and 0-5 bamboo condition had not significant negative effect on understory species diversity in* A. faxoniana *forest. We suggest the fine-scale analysis on effects of bamboo abundance should be taken account into considering in heterogeneous patches in process of the succession and regeneration of natural forests.*

Keywords: Bamboo abundance; Fargesia nitida*; relative photosynthetic photon flux density; species diversity*

ABSTRAK

Buluh kerdil diiktiraf sebagai penentu penting struktur dan dinamik dalam hutan beriklim sederhana. Hubungan kuantitatif antara kelimpahan (kepadatan dan liputan) buluh kerdil, Fargesia nitida*, dan mikro-persekitaran, kepelbagaian spesies di atas lantai telah dianggarkan dalam hutan* Abies faxoniana *tulen di barat daya China. Keadaan mikro alam sekitar mikrokanopi bawahan (harian perbezaan suhu dan kelembapan, RPPFD di bawah lapisan buluh dan penutup bumi) telah berubah dengan dramatik dengan kepadatan buluh. Analisis regresi langkah demi langkah berbilang menunjukkan bahawa kelimpahan* F. nitida *terutamanya berkait rapat dengan ciri-ciri kanopi dan faktor-faktor gangguan dalam hutan* A. faxoniana *tulen. Semua indeks kekayaan menurun dengan ketara dengan kepadatan buluh dan RPPFD di bawah lapisan buluh. Kepentingan nilai-nilai (IV) spesies bawah kanopi dalam kepadatan yang berlainan buluh dan analisis kesetaraan kanun Detrended (DCCA) menunjukkan tiga kumpulan tumbuhan bawahan, tahan pintas kepada kelimpahan buluh tinggi (Kumpulan A), tahan banyak buluh sederhana (Kumpulan B) dan sensitif terhadap banyak buluh (Kumpulan C). Kumpulan-kumpulan ini terutamanya memberi respon terhadap banyak buluh dan RPPFD di bawah lapisan buluh, hasil daripada padat integrasi ciri-ciri faktor buluh, kanopi dan topografi. Banyak buluh yang berlainan mempunyai pengaruh yang berbeza pada kepelbagaian spesies bawahan dan kumpulan. Keadaan* F. nitida *padat (> 10 culms/mz) mempunyai kesan negatif yang ketara dan 0-5 keadaan buluh tidak mempunyai kesan negatif yang besar ke atas kepelbagaian spesies bawahan di hutan* A. faxoniana. *Kami mencadangkan analisis yang skala kecil ke atas kelimpahan perlu diambilkira ke dalam mempertimbangkan dalam tompok heterogen dalam proses penggantian dan pertumbuhan semula hutan semula jadi.*

Kata kunci: Kelimpahan buluh; Fargesia nitida*; ketumpatan fluks relatif foton fotosintesis; kepelbagaian spesies*

INTRODUCTION

Plants of the forest understory modified the forest floor micro-environment, which plays an important role in controlling the forest composition, species diversity and regeneration undergrowth in many forests (George & Bazzaz 1999; Itô & Hino 2007). In East Asia, it was well-known that dwarf bamboos, a typical understory plant with the wide distribution and exclusive density, could inhibit survival and regeneration of tree seeds (Iida 2004), seedlings and saplings (Taylor et al. 2004), mature trees (Takahashi et al. 2003), and understory plant genetic diversity (Wang et al. 2012) and species diversity (Wang et al. 2007) in both Chinese and Japanese forests. However, some studies showed a certain density of dwarf bamboos might had positive, indirect effects. The distribution of dwarf bamboo could inhibit the bark-stripping or grazing on tree species by forest ungulates (Itô & Hino 2005).

Most previous studies above were focused on the responses of species regeneration and understory species diversity to the presence or absence of dwarf bamboo (Caccia et al. 2009), rather than the responses to continuous variation of dwarf bamboo and the cause for this different response. In forest understory, radiation intensity (i.e. Photosynthetic Photon Flux Density-PPFD) and other microclimatic factors played a major role in the growth, survival, and regeneration of understory species (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 the coexistence of diverse species, the advanced regeneration and newly regenerated individuals in different ecosystems (George & Bazzaz 1999; Wang et al. 2008). Therefore, that is a key to discussing the influence of variation in forest floor conditions with abundance of dwarf bamboo, on understory species diversity, and to understanding the quantitative relationships between understory species diversity and abundance of dwarf bamboo.

Abies faxoniana is a representative evergreen conifer species, which commonly form a pure stand in the subalpine forest, southwest China. *Fargesia nitida* (Mitford) Keng f. et Yi, commonly dominate in forest understories of *A. faxoniana* pure forest (Wang et al. 2009). Our previous study revealed that dense *F. nitida* had negative effect on understory diversity of shrub and regeneration of *A. faxoniana* (Wang et al. 2007). However, we have not documented the variation of micro-environments on the floor with abundance of *F. nitida* and the responses of species composition and diversity to abundance of *F. nitida*.

In this study, our objectives were to understand how different abundance of *F. nitida* affects understory species diversity and groups in this region. We specifically discuss the following questions: (1) What are significant variations of micro-environments on the floor with bamboo abundance?, (2) The relationship between bamboo abundance and understory species diversity?, and (3) What are the adaptation and response of understory species composition to variation in bamboo abundance?

MATERIALS AND METHODS

STUDY AREA

The study site was located in a subalpine dark coniferous forest near 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, southwest China. The annual mean temperature is 4.3 °C, and the annual precipitation and annual evaporation capacity is about 848.9 mm and 772.5 mm, respectively. The annual sunshine duration lasts approximately 1185.4 h (Li et al. 2007).

The forest on the site mainly consists of evergreen coniferous tree species *A. faxoniana*, with sporadic distribution of deciduous broadleaved trees *Betula utilis* and *Acer caudatum*, and the forest floor is mainly covered with *F. nitida*, with the height about 1.5 m to 3.0 m (Li et al. 2007).

DATA COLLECTION

Measurement of community was mainly conducted in *A. faxoniana* pure forest, in which extended gap (EG)> 50 m^2 was excluded (Wang et al. 2009), in mid-summer (August 2006). Two parts of 65 adjacent plots (each 10 m × 10 m, 6500 m^2 in total) were sampled (Figure 1(e)). Each plot (100 m^2) was composed of 4 quadrats of 5 m × 5 m. For each quadrat, height, basal diameter, coverage of each tree and each shrub, and average height and coverage of each herb in a random 1 m × 1 m small quadrat within each quadrat were measured. Coverage of shrub and herb layer, and culm density (culms/m^2) and coverage of the bamboo were recorded in each quadrat.

The number of fallen trees (diameter at breast height (DBH) > 20 cm) and broken branches (DBH < 10 cm) were investigated on the floor of each plot (Wang et al. 2009). Broken branches included big broken branches (10 cm > DBH > 5 cm) and small broken branches (DBH < 5 cm). Topographical factor, elevation, slope, slope aspect and position were recorded in each plot. Seven, five, three, and one were evaluated to the position, namely, upper, middle, lower and flat slope (Wang et al. 2006). The slope aspect was evaluated according to our previous study (Wang et al. 2009). Other factors in DCCA analysis were measured values.

Canopy density was measured by the LAI-2000 Plant Canopy Analyzer (LI-COR Lincoln USA) set up above shrub layer in the middle of each plot. PPFD was simultaneously measured on several overcast days in August 2006 under the canopies and over the canopies in the centre of each plot respectively by two LI-191SA Line Quantum Sensors (LI-COR Lincoln USA) and was recorded by LI-1400 and LI-2000 Data Loggers (LI-COR Lincoln USA). PPFD under the canopies was measured over (height = 3 m above the ground) and under (height = 0.5 m above the ground over herb layer) the layer of *F. nitida*. Relative photosynthetic photon flux density (RPPFD) over bamboo and under bamboo within each plot was then calculated.

In each plot, air temperature and moisture meters were used to measure the air temperature and moisture, respectively at 0.5 m above the ground. Soil temperature meter was put on the surface of soil to measure temperature of soil surface. From July 27 to August 8, 2006 (four clear days), the measurements were conducted at 2 h intervals four the whole day to calculate daily differences of air temperature and moisture, and temperature of surface soil.

In each plot, mean values of thickness of litters, bryophytes and soil humus on the ground were calculated base five random samples.

DATA ANALYSIS

The importance values (IV) of species were calculated using the following formulas (Wang et al. 2009): IV shrub and herb = (relative height + relative coverage +relative frequency) ×100/3.

Species diversity is the species richness understory of plot, including total, woody and herbaceous species richness.

Detrended canonical correspondence analysis (DCCA) of CANOCO4.5 soft was used to analyze the relationship between distribution of understory species (based on importance values) and environmental variables in each plot, and to discussing understory species group classification (Wang et al. 2009). Stepwise multiple regression was employed to find the main factors influencing the abundance of *F. nitida* and understory species diversity, and One-way ANOVA were carried out to compare understory micro-environmental factors and species diversity in different bamboo densities by SPSS 11.0 statistical package (SPSS 11 Copyright: SPSS Inc.). The figures were drawn by OriginPro 7.0.

Results

MICRO-ENVIRONMENTAL CONDITIONON THE FLOOR

Canopy density, RPPFD over bamboo layer (under the canopy), density and coverage of *F. nitida* were described in different classes in each plot of *A. faxoniana* pure forest (Figure. 1a-d).

Stepwise multiple regression analyses showed that density of *F. nitida* decreased significantly with no. of big broken branches and fallen trees, and canopy density in all plots. Coverage of *F. nitida* decreased significantly with no. of small broken branches and RPPFD over bamboo layer (under the canopy) (Table 2). Abundance of *F. nitida* was mainly correlated with canopy characteristics and disturbance factors in the *A. faxoniana* pure forest.

The percentage areas of the bamboo densities class within the *A. faxoniana* forest were 15-20 and 20-25 class both 9.23% (6 plots), non-bamboo (0 class) 10.77% (7 plots), 0-5 and 10-15 class both 12.31% (8 plots), 5-10 class 18.46% (12 plots), and above 25 class 27.69% (18 plots) (Figure. 2a). RPPFD under bamboo layer decreased with the bamboo density. RPPFD had significant differences between over and under bamboo layer in all bamboo classes except in 0 and 0-5 class. RPPFD under bamboo layer could be less than 5% at bamboo density > 10 culms/m^2 (Figure. 2b).

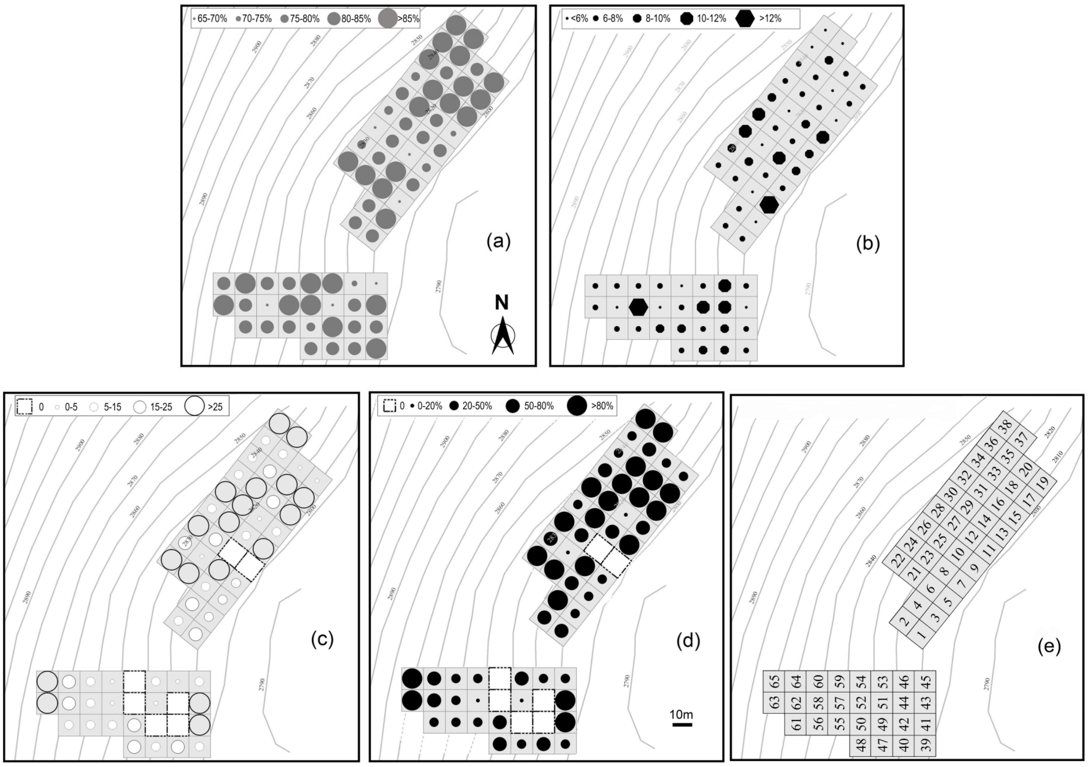

FIGURE 1. Canopy conditions (a, b), the abundance of *Fargesia nitida* (c, d) and plot number (e) in an *Abies faxoniana* pure forest. Size of circle and polygon indicates different canopy density (a) and RPPFD over bamboo layer (under the canopy)(b), and culm density (c) and coverage (d) of this bamboo species in each plot. Square with broken lines means no distribution of *Fargesia nitida*

The daily differences of air temperature and moisture, and temperature of surface soil decreased with the bamboo density. Thickness of bryophytes decreased, and thickness of litters and soil humus increased with the bamboo density (Table 1).

SPECIES DIVERSITY AND GROUPS ON THE FLOOR

In general, understory total species richness, woody richness and herbaceous richness decreased with the bamboo density. However, these indices had no significant differences between 0 and 0-5, and between 5-10 and 10-15 bamboo class (Figure 3).

Stepwise multiple regression analyses indicated that all richness indices decreased significantly with the bamboo density in all plots. Understory total species richness also decreased significantly with bamboo coverage and increased with RPPFD under bamboo layer. Understory woody richness also increased significantly with total broken branches and RPPFD under bamboo layer. Understory herbaceous richness also increased significantly with daily moisture differences (Table 2).

In shrub layer, dominance of *A. faxoniana* decreased with the bamboo density. *Euonymus stenophyllus* and *E. przwalskii* was dominant in bamboo densities of >25 and

TABLE 1. Features of forest floor in different bamboo densities of *A. faxoniana forest*

Features of forest floor	Densities class of *Fargesia nitida*						
	0	0-5	5-10	10-15	15-20	20-25	>25
Daily temperature differences of air (°C)	15.33(0.31)^a	15.02(0.32)^a	12.27(0.39)^b	11.91(0.35)^b	10.26(0.43)^c	9.78(0.19)^c	7.72(0.15)^d
Daily moisture differences of air (%)	43.17(0.29)^a	40.11(3.13)^a	36.02(0.76)^b	30.54(0.90)^c	29.59(0.49)^c	28.02(0.20)^c	18.45(0.92)^d
Daily temperature differences of surface soil (°C)	10.12(0.23)^a	10.21(0.24)^a	8.44(0.28)^b	7.82(0.47)^b	7.11(0.43)^b	6.13(0.29)^c	5.42(0.11)^d
Thickness of litters (cm)	0.34(0.09)^d	0.48(0.16)^d	0.54(0.15)^d	2.02(0.33)^c	2.67(0.39)^c	3.44(0.21)^b	4.52(0.27)^a
Thickness of bryophytes (cm)	4.95(0.51)^a	3.88(0.30)^a	1.78(0.29)^b	0.38(0.09)^c	0.03(0.01)^d	0^d	0^d
Thickness of soil humus (cm)	5.20 (0.46)^d	5.84(0.35)^d	8.43(0.32)^c	9.66(0.39)^b	10.12(0.34)^b	12.02(0.28)^a	12.52(0.31)^a

Data are mean (standard error)

Different letters indicate significant differences at $P < 0.05$ level in different bamboo conditions.

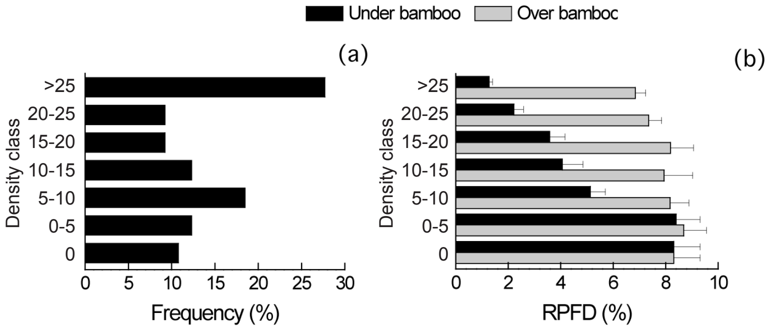

FIGURE 2. (a) Frequency distribution and (b) RPPFD over and under bamboo layer in different densities class of *Fargesia nitida* in *Abies faxoniana* pure forest. Error bars are standard error, the same below

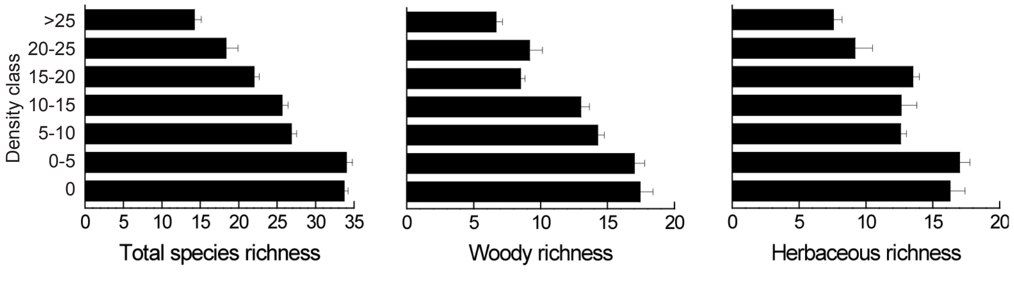

FIGURE 3. Understory total species richness, woody richness and herbaceous richness in different densities class of *Fargesia nitida* in *Abies faxoniana* pure forest

TABLE 2. Results of stepwise multiple regression analysis, conducted separately for abundance of fargesia nitida and understory species diversity

Parameters		Canopy disturbance				Canopy characteristics		Micro-environments on the floor		Bamboo		P	r^2
		Small broken branches	Big broken branches	Total broken branches	Fallen trees	Over RPPFD	Canopy density	Daily moisture differences	Und RPPFD	Density	Coverage		
Abundance of *Fargesia nitida*	Density	–	–0.142 (0.018)	–	–0.160 (0.009)	–	–0.151 (0.011)	/	/	/	/	<0.001	0.684
	Coverage	–0.562 (0.000)	–		–	–0.211 (0.039)	–	/	/	/	/	<0.001	0.730
Understory species diversity	Total richness	–	–	–	–	–	–	–	0.158 (0.036)	–0.574 (0.000)	–0.276 (0.002)	<0.001	0.911
	Woody richness	–	–	0.187 (0.002)	–	–	–	–	0.114 (0.041)	–0.672 (0.000)	–	<0.001	0.828
	Herbaceous richness	–	–	–	–	–	–	0.304 (0.000)	–	–0.684 (0.000)	–	<0.001	0.903

Results (data from all plots), using the Standardized coefficients (with P values in parentheses) for the selected variables, P value of the model and r^2 are shown for each model. See Table 1 for the abbreviations of *F. nitida* characteristics.

TABLE 3. Important Value of understory dominant species (IV > 1) in different bamboo densities class in *Abies faxoniana* pure forest

Understory dominant species	Important value in different density class of *Fargesia nitida*						
	>25	20-25	15-20	10-15	5-10	0-5	0
wood							
Fargesia nitida	69.45	52.67	46.93	36.65	27.38	8.91	/
Acer caudatum	0.80	1.74	0.33	4.95	5.07	1.78	1.19
Smilax stans	/	/	/	0.56	/	4.05	5.71
Sorbus koehneana	/	/	/	3.69	4.70	4.01	2.56
Smilax china	4.25	2.76	2.89	3.47	4.10	6.17	11.72
Euonymus przwalskii	1.50	9.84	8.24	1.30	4.80	4.10	4.91
Euonymus stenophyllus	10.54	4.74	1.82	3.34	3.47	2.26	2.70
Abies faxoniana	1.97	6.08	6.92	11.42	11.91	21.49	18.59
Viburnum betulifolium	0.46	4.58	6.97	2.85	2.16	2.37	5.32
Rosa omeiensis	/	2.46	2.25	3.87	3.30	6.45	4.31
Lonicera lanceolata	1.07	4.13	5.28	4.75	4.19	3.04	7.05
Lonicera tangutica	/	3.68	4.59	5.85	5.69	1.94	3.82
Rhododendron agglutinatum	0.60	4.24	2.11	2.51	3.76	2.31	1.46
Berberis jamesiana	1.24	/	/	0.33	0.25	10.04	8.82
Lonicera microphylla	/	2.92	3.31	2.16	2.37	2.34	1.90
Betula utilis	/	/	/	3.35	3.04	5.73	6.54
Ribes glaciale	/	/	/	3.05	3.56	1.58	0.46
Hydrangea xanthoneura	/	/	/	3.37	3.85	2.22	7.79
Cotoneaster apiculatus	/	/	/	/	/	8.95	3.78
Herb							
Oxalis corniculata	0.64	6.62	7.66	6.41	6.16	2.57	1.64
Fragaria orientalis	/	/	/	1.18	/	4.44	3.83
Parasenecio otopteryx	0.58	10.69	8.07	13.20	13.79	10.54	6.40
Stellaria media	2.11	8.08	8.21	3.54	4.15	2.58	4.38
Cystopteris montana	4.33	7.66	10.64	8.90	7.13	5.53	10.45
Rodgersia podophylla	/	/	/	/	/	2.08	3.24
Saxifraga stolonifera	15.10	/	/	0.74	/	/	2.37
Smilacina henryi	/	/	/	/	/	1.33	1.62
Dryopteris rosthornii	0.59	11.34	11.38	3.59	1.04	6.90	2.93
Elatostema macintyrei	20.41	13.50	14.38	9.27	12.16	5.65	1.17
Allium ovalifolium	/	7.30	4.54	6.18	5.09	3.98	4.10
Pseudostellaria davidii	2.31	/	/	/	/	1.84	3.85
Streptopus obtusatus	/	10.27	8.23	4.86	7.60	2.82	4.60
Parasenecio profundorum	15.82	7.02	10.64	9.77	9.89	8.49	1.50
Carex infuscata var. gracilenta	35.06	/	/	4.07	3.10	5.56	5.28
Ctenitis sp.	1.35	6.96	5.48	12.29	11.78	11.53	3.01
Ligularia hodgsonii	/	/	/	/	/	0.45	1.80
Parasenecio palmatisecta	1.17	6.86	3.99	11.28	11.54	10.86	12.87
Parasenecio souliei	/	/	/	/	2.56	10.89	17.51

15-25 culms/m^2, respectively. *Lonicera lanceolata* and *L. tangutica* had higher dominance in moderate bamboo density (5-15 culms/m^2). *Smilax stans*, *Betula utilis*, *Hydrangea xanthoneura* and *Cotoneaster apiculatus* had no distribution at bamboo density > 15 culms/m^2. In herb layer, *Carex infuscata*, *Parasenecio profundorum*, *Elatostema macintyrei* and *Saxifraga stolonifera* were dominant in the highest bamboo density. Dominance of *E. macintyrei* increased with the bamboo density. *P. palmatisecta* and *P. souliei* were dominant at bamboo density < 5 culms/m^2. *Oxalis corniculata*, *P. otopteryx*, *Dryopteris rosthornii*, *Streptopus obtusatus*, *Stellaria media* and *Ctenitis* sp. had higher dominance in moderate densities of bamboo (5-20 culms/m^2) (Table 3).

The first DCCA axis showed the variation of understory micro-environment conditions, which reflected the density and coverage of *F. nitida* decreased, and the understory RPPFD (to some extent, with small broken branches)

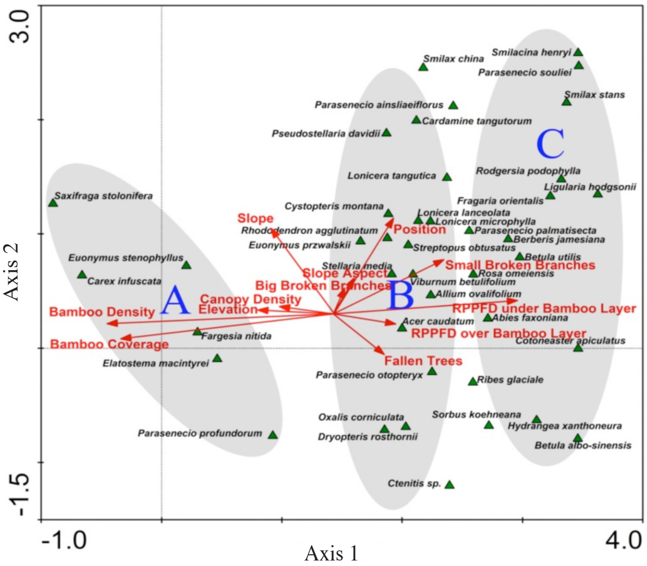

FIGURE. 4 DCCA ordination of the *Abies faxoniana* pure forest based on the understory species matrix of 41 species and 65 plots, and on the environment matrix of 11 factors (4 community characteristics, 4 topography factors and 3 disturbance factors) and 65 plots. Different gray ellipses with letters mean different understory plant groups, and green triangle with labels mean different species.

increased from left to right. The first DCCA axis meanly indicated the variation of bamboo abundance. The second axis of DCCA revealed the change of topography that slope and position facing south increased from bottom to top (Figure 4).

According to DCCA ordination and the dominance of understory species in different bamboo densities class (Table 3), the plant groups responded to the variation of understory micro-environment conditions, mainly to abundance of bamboo, were classified into three plant groups (Figure 4).

Group A: resistant to high bamboo abundance. This type was positively related to bamboo abundance and negatively related to understory RPPFD. It was located at the left of the DCCA axis and dominated in high bamboo abundance. *E. stenophyllus, C. infuscata, P. profundorum, E. macintyrei* and *S. stolonifera* were the typical species.

Group B: resistant to intermediate bamboo abundance. This type dominated in intermediate of many understory micro-environment factors, including bamboo abundance. It was located in the center of the DCCA axis, which showed that resistant to intermediate disturbance in bamboo conditions. The typical species included *E. przwalskii*, *L. lanceolata*, *L. tangutica*, *O. corniculata*, *P. otopteryx*, *D. rosthornii*, *S. obtusatus*, *S. media* and *C.* sp.

Group C: sensitive to bamboo abundance. This type was negatively related to bamboo abundance and positively related to understory RPPFD. It was located at the right of the DCCA axis and only distributed or dominated in low and no bamboo abundance. *A. faxoniana*, *B. utilis*, *P. palmatisecta*, *P. souliei*, *Smilax stans*, *H. xanthoneura* and *C. apiculatus* were the typical species.

DISCUSSION

RELATIONSHIP BETWEEN CANOPY CHARACTERISTICS AND UNDERSTORY BAMBOO

Stepwise multiple regression analyses showed abundance (density and coverage) of *F. nitida* was mainly correlated with canopy characteristics (canopy density and RPPFD over bamboo layer) and disturbance (broken branches and fallen trees) in the *A. faxoniana* pure forest (Table 2). This high relationship between forest canopy characteristics and forest understory plants were reported in many temperate forests (Taylor et al. 2004). Natural disturbances, such as wind, fire, plant diseases and insect pests, and trees decline and fall, were viewed as important factors to tree species, especially for *A. faxoniana* (Wang et al. 2009). Broken branches and fallen trees were commonly occurred by these canopy disturbances in this region, which further influenced understory species. Simultaneously, broken branches, canopy density and light condition had significant influenced the density and coverage of dwarf bamboo in subalpine forest in previous study (Noguchi & Yoshida 2005; Suzaki et al. 2005; Wang et al. 2009). Therefore, forest canopy composition, density and disturbance affect patterns of resource availability (i.e. light, precipitation, soil nutrients) and conditions of broken branches and fallen trees on the forest floor which, in turn, influence the abundance of understory bamboo.

THE EFFECTS OF BAMBOO ABUNDANCE

In *A. faxoniana* pure forest with widespread dwarf bamboo in this region (Figure 1 and 2(a)), understory micro-environmental conditions (daily differences temperature and moisture, RPPFD under bamboo layer and ground cover) changed dramatically with the bamboo density. These changes might influence the habitat conditions of many understory species.

The effects on species composition and diversity

F. nitida had a negative effect on understory species diversity when the density was > 5 culms/m^2. This negative effect increased with the bamboo density, and could be resulted from the significant variations in understory micro-environmental conditions with bamboo abundance.

Stepwise multiple regression analyses indicated that understory species diversity was negatively correlated to bamboo abundance and RPPFD under bamboo layer (Table 2). Density and coverage of bamboo mainly influenced RPPFD on the floor, which was determinant to survival and growth of understory plants (Caccia et al. 2009; Taylor et al. 2004). The amount of light reaching the forest floor differed widely among different bamboo densities, from less than 3% RPPFD at bamboo density > 20 culms/m^2, to about 8% RPPFD at bamboo density < 5 culms/m^2 and no bamboo condition, and RPPFD under bamboo layer could be less than 5% at bamboo density > 10 culms/m^2. Some researchers found most species (even the shade tolerant species) developed poorly and could be limited at RPPFD < 3% and could not be survived at RPPFD < 5% in simulated experiments (Emborg 1998; Madsen 1995). Moreover, the RPPFD threshold for species survival is much higher under wild additional stress from water, nutrients, fungi, insects, and competition etc. (Emborg 1998). Only some species, typical extremely shade tolerance lianas *Euonymus* genus (commonly growing under dense forest canopy), *E. stenophyllus*, *E. przwalskii* and shade tolerance herb *S. stolonifera*, *C. infuscata*, *P. profundorum*, *E. macintyrei* distributed in dense bamboo condition (Wu et al. 2007).

Dense culms and rhizomes anfractuosity of *F. nitida* (bamboo density > 10 culms/m^2) invaded and occupied the above-ground and under-ground growth space, which lead other shrubs and herbs have no space to live (Wang et al. 2007). Thick litters of *F. nitida* (Thickness > 2 cm at bamboo density > 10 culms/m^2) in surface soil also restricted seed regeneration of wood species and survival of herbs (Wang et al. 2007). Thus, strong regeneration space (above-ground and below-ground space) competition decreased the species diversity understory (Wang et al. 2008). These results were consistent with many studies on the negative effect of dwarf bamboo on undergrowth species diversity (Noguchi & Yoshida 2005; Wang et al. 2007).

However, micro-environments under bamboo layer and all species richness indices had no significant differences between 0 and 0-5 bamboo density condition. The 0-5 density class of *F. nitida* condition had no significant negative effect on understory species diversity. As no bamboo condition, RPPFD in 0-5 bamboo condition (about 8%) (Figure 2) may afford micro-habitats to both extremely shade-tolerant and other species, especially for herbs (Emborg 1998). Little litters on surface soil were helpful to seed germination, growth of plants and propagation of some species. Thick bryophytes reflected strong water retaining capacity for growth of plants on the floor (Li et al. 2006).

The response of species groups to bamboo abundance

The adaptation of understory species to the similar micro-environments on the floor suggested the response to understory bamboo abundance and disturbance of broken branches (Wang et al. 2006). According to DCCA ordination and explanation of first Axis, three plant groups were reflection to the variation of bamboo abundance. Group A was the response type to high abundance of *F. nitida*. The species in the left side of DCCA figure were the key positive indicator species for high bamboo abundance. They were typical species adapting to extreme environments, might be extremely shade tolerance lianas *Euonymus* genus (*E. stenophyllus*) and shade tolerance herb *S. stolonifera*, *C. infuscata*, *P. profundorum*, and *E. macintyrei*, with high net photosynthetic rate, stomatal conductance and chlorophyll content, and low chlorophyll a/b (Wu et al. 2007). Group B was he response type to moderate abundance of *F. nitida*. The species in the middle of DCCA figure, such as *E. przwalskii*, *L. lanceolata*, *L. tangutica*, *O. corniculata*, *P. otopteryx*, *D. rosthornii*, *S. obtusatus* (having wider ecological amplitude and adaptation). Group C was the response type to low abundance and no *F. nitida*. The species in the right side of DCCA figure, which indicated the adaptation to low abundance and no bamboo condition, and to strong disturbance of broken branches of *A. faxoniana*. Type species included *A. faxoniana*, *B. utilis*, *P. palmatisecta*, *P. souliei*, *Smilax stans*, *H. xanthoneura* and *C. apiculatus*. The demand for light in (*Abies alba*) increased with the age (1 yr, 2 yr, 5 yr and 5-15 yr required 1.7-2.7%, 5%, 8% and 15%-25% RPFD, respectively (Lin & Liu 2008; Robakowski et al. 2003). Thus, low light condition under dense *F. nitida* was key determinant to regeneration of *A. faxoniana* (Robakowski et al. 2003). *C. apiculatus* was the key positive indicator species for no bamboo condition.

CONCLUSION

Therefore, different understory species groups could be identified in different bamboo abundance in the *A. faxoniana* pure forest. Each group might be determined by bamboo abundance and RPPFD under bamboo layer resulted from integrative effects of bamboo density, canopy characteristics and canopy disturbance, slope, position and other factors.

Different bamboo abundance had different influence on understory species diversity and groups. In dense *F. nitida* condition (> 10 culms/m^2), low RPPFD, high thickness of litters, dense culms and anfractuosity of their rhizomes restricted the dominant and survival of species understory. 0-5 bamboo condition had not significant negative effect on maintenance of species diversity in *A. faxoniana* forest.

We suggest the fine-scale analysis on effects of bamboo abundance should be taken account into considering in heterogeneous patches in process of the succession and regeneration of natural forests. Further studies on dynamic of bamboo abundance (such as developing, sporadic flowering or by disturbance) can helpful to understanding understory environmental changes, and species dynamics and regeneration of *A. faxoniana* forest in this region.

ACKNOWLEDGEMENT

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).

REFERENCES

Caccia, F.D., Chaneton, E.J. & Kitzberger, T. 2009. Direct and indirect effects of understory bamboo shape tree regeneration niches in a mixed temperate forest. *Oecologia* 161: 771–780.

Emborg, J. 1998. Understory light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology Management* 106: 83–95.

George, L.O. & Bazzaz, F.A. 1999. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology* 80:846–856.

Iida, S. 2004. Indirect negative influence of dwarf bamboo on survival of *Quercus* acorn by hoarding behavior of wood mice. *Forest Ecology Management* 202: 257–263.

Itô, H. & Hino, T. 2005. How do deer affect tree seedlings on a dwarf bamboo-dominated forest floor. *Ecological Research* 20: 121–128.

Itô, H. & Hino, T. 2007. Dwarf bamboo as an ecological filter for forest regeneration. *Ecological Research* 22: 706–711

Li, F.X., Wang, Y.F., Zhan, Q.F., Xu, B., Zhai, D.C. & Dang G.D. 2006. Species diversity of floor bryophyte communities in Foping Nature Reserve. *Chinese Journal of Plant Ecology* 30: 919–923.

Li, Y., Tao, J.P., Wang, Y.J., Yu, X.H. & Xi, Y. 2007. Effects of *Fargesia nitida* on regeneration of *Abies faxoniana* seedlings near the edge of subalpine dark coniferous forest. *Chinese Journal of Plant Ecology* 31: 283–290.

Lin, B. & Liu, Q. 2008. Plasticity responses of 4 tree species in subalpine-coniferous-forest to different light regimes. *Acta Ecologica Sinica* 28: 4665–4675.

Madsen, P. 1995. Effects of soil water content, light, fertilization, weed competition and seedbed type on natural regeneration of beech (*Fagus sylvatica*). *Forest Ecology Management* 72: 251–264.

Messier, C., Parent, S. & Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9: 511–520.

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 Forest* 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. *Ecological Research* 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.

Suzaki, T., Kume, A. & Ino, Y. 2005. Effects of slope and canopy trees on light conditions and biomass of dwarf bamboo under a coppice canopy. *Journal of Forest Research* 10: 151–156.

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. *Ecological Research* 18: 767–774.

Taylor, A.H., Huang, J.Y. & Zhou S.Q. 2004. Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies– Betula* forests in southwestern China: a 12-year study. *Forest Ecology Management* 200: 347–360.

Wang, Y. J., Shi, X. P. & Zhong, Z. C. 2012. Clonal Diversity and Genetic Differentiation in Rhizomatous Herb, *Iris s. japonica* (Iridaceae) Populations on Jinyun Mountain, Southwest China. *Sains Malaysiana* 41(2): 149-154.

Wang, Y.J., Tao, J.P., Li, Y., Yu, X.H. & Xi, Y. 2007. Effects of *Fargesia nitida* on species diversity and trees regeneration in different forest cycles of subalpine forest in Wolong Nature Reserve. *Scientia Silvae Sinicae* 43(2): 1–7.

Wang, Y.J., Tao, J.P., Zhang, W.Y., Zang, R.G., 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 Ecologica Sinica* 26: 3525–3532.

Wang, Y.J., Tao, J.P. & Zhong, Z.C. 2009. Factors influencing the distribution and growth of dwarf bamboo, *Fargesia nitida*, in a subalpine forest in Wolong Nature Reserve, southwest China. *Ecological Research* 24: 1013–1021.

Wang, Y.J., Zhong, Z.C. & Tao, J.P. 2008. Patterns of ramet population of *Iris japonica* Thunb. and their effects on herb diversity in different microsites on Jinyun Mountain. *Acta Ecologica Sinica* 28: 3082–3091.

Wu, L., Zhu, H., Lu, Y.J. & Gao, Y.H. 2007. Resource status of the ground cover plants and potential analysis of exploitation and utilization in Hangzhou city. *Scientia Silvae Sinicae* 43(8): 60–64.

Yong-Jian Wang & Xue-Ping Shi
College of Horticulture & Forestry Sciences
Huazhong Agricultural University
Wuhan 430070
China

Yue Peng
Chongqing Academy of Forestry Science
Chongqing 400036
China

Zhang-Cheng Zhong & Jian Ping Tao*
Key Laboratory of Eco-environments of Three Georges Reservoir Region (Ministry of Education) of Southwest University
Chongqing 400715 China

*Corresponding author; email: wangyj@mail.hzau.edu.cn / taojp@swu.edu.cn

Received: 13 September 2011
Accepted: 22 December 2011