

Juan YANG, Jianping GE, Lijuan LIU, Yi DING, Yingchun TAN

# Gap phase regeneration recruitment of mixed conifer-broadleaf forests in Wolong Nature Reserve

© Higher Education Press and Springer-verlag 2009

**Abstract** Wolong Nature Reserve is the largest reserve for protecting the endangered wild giant panda. Due to historical factors, even in many sections of the core protection area, the forests have been seriously destroyed and natural forests are poorly restored. However, the relative importance of the determinants for recruitment of communities under disturbance is rarely explored. In our study the endogenous and exterior factors in a forest gap that affect the conifer-broad-leaved mixed forest regeneration were investigated near Wuyipeng, one of the observation stations at Wolong, to explore which determinant had the greatest effect on gap regeneration and to discover the recruitment of seedling establishment in forest gaps. With a linear sampling method, environmental factors, gap characteristics and recruitment of new individuals were measured and examined in every forest gap along three sampling lines. Data of environmental factors in the gaps were collected for a Pearson correlation analysis in order to explore the disturbance and pre-processed characteristics of the gaps, using principal component analysis in SPSS. Correlation analysis was applied to further explore the relationship between changes in the gaps and the response of the regenerating seedlings. The results show that a range of natural and human disturbances affected the pattern and characteristics of the forest gaps in this area. The richness in the composition

of the seedlings was higher than that of gap makers, but the order of dominance of the composition was different between seedlings and gap makers. The success of dominant species in establishing themselves was affected by different environmental factors. For instance, the establishment of *Betula* spp. was correlated significantly with topographic factors, while that of *Abies faxoniana* was affected by soil characteristics and that of *Rhododendron* spp. correlated significantly with topographic factors and characteristics of gap makers. Moreover, all the biodiversity indices of regenerating seedlings were significantly correlated with environmental principle components mostly reflecting soil properties. From this we can infer that soil characteristics are the most important factors affecting the regeneration of dominant species and seedling diversity under gap disturbances.

**Keywords** gap regeneration, gap maker, biodiversity index, principle component analysis, correlation analysis

Translated from *Journal of Plant Ecology (Chinese Version)*, 2007, 31 (3): 425–430 [译自: 植物生态学报]

Juan YANG  
School of Marine Science, China University of Geosciences, Beijing 100083, China

Jianping GE (✉), Lijuan LIU  
College of Life Sciences, Beijing Normal University, Beijing 100875, China  
E-mail: gejp@bnu.edu.cn

Yi DING  
College of Life Sciences, Southwest University, Chongqing 400715, China

Yingchun TAN  
Research and Conservation Center for the Giant Panda, Wolong 623006, China

## 1 Introduction

According to forest cycle theories, natural disturbances, especially small ones, play a very important role in the maintenance of forest canopy structures. Canopy gaps have become major opportunities for protection and preservation of forest biodiversity (Zang et al., 1999a). In recent years, as concepts and methodologies are improving, investigations in gap dynamics have been widely launched, and on occasion have been responsible for the enormous progress in the temperate and tropical forests (Brokaw, 1985; Schupp, 1989; Spies and Franklin, 1989). Research in the gaps has also gradually been extended to savannas (Rebertus and Burns, 1997), mangroves (Duke, 2001) and other types of communities. Since the early 1990s, some Chinese scholars have also been involved in this area. Their research covers a large range of forest types in China, such as broad-leaved Korean pine forests in northeastern China, dark coniferous forests, subtropical evergreen broad-leaved forest, tropical mountain forests and subalpine forests, as well as in many solid research aspects, including the characteristics of forest gaps, gap

interference patterns, gap responses to forest species, the relationship between gap dynamics and biological diversity, gap dynamics simulation and others (Shao et al., 1989; Yu and Zhao, 1997; Wu et al., 1999; Wu, 1999; Zang et al., 1999b; Shen et al., 2001; Luo et al., 2002; Yang, 2002; Wang et al., 2003). These studies provide large amounts of evidence supporting the idea that most forest regeneration, occurring in canopy gaps and natural succession, is frequently driven by small-scale disturbances. Their research achievements also provide further ideas in scientific explorations in forest biodiversity conservation and sustainable utilization of Chinese forest resources.

As an important part of the habitat for the wild Giant Panda, the forest vegetation dynamics in the Wolong Nature Reserve significantly affects the survival and propagation of this endangered animal. The conifer-broad-leaved mixed forest around Wuyipeng, one of the field observations posts for the Giant Panda, denotes the typical conditions in the habitat of the Giant Panda, where the forest communities have been seriously damaged with the passage of time and the most dominant tree species are old growths, severely diseased and suffer from poor natural recovery. As one of the most important places of local natural regeneration, forest gaps were early observed by Taylor and Qin (1988). They considered that in this study area, canopy gaps are filled primarily by new arrivals and not by suppressed seedlings or saplings from the understory. Population recruitment of *Abies faxoniana* and *Betula utilis* is most frequently associated with small disturbances such as a tree fall. Therefore, the size of the canopy gap was presumed to be one of the major factors that affected gap regeneration patterns and seedling biodiversity in our study area. Except for this, Runkle (1985) believed that the potential light in canopy gaps increases with the ratio of crown gap diameter to height, which further impacts the microclimate and the response of regenerating seedlings to forest gaps. Moreover, less shade-tolerant tree species were always overwhelming in gap regeneration in the case where one large tree had collapsed, while more shade-tolerant tree species may be dominant when many small trees collapse at the same time (Veblen, 1992). That means that the characteristics of these gap makers, such as the number and composition of recruitment and diameter class distribution, are also significant factors that impact gap regeneration. Apart from micro-environmental changes occurring after gap formation, site conditions, such as topography and soil properties, also affect gap regeneration but in a more random fashion. In other words, tree species may respond differently given the background of the microhabitat and may change after gap formation, resulting in different refilling patterns. A more recent study has illuminated the gap interference characteristics in our study area (Yang, 2004).

Given our in-depth survey of gap regeneration, we discuss seedling abundance of the dominant species and

species diversity of seedlings responding to gap interference. The most likely community succession after gap disturbance was expected to be displayed and guidance to be provided for native forest restoration and protection of the habitat of the wild Giant Panda.

---

## 2 Study area

The Wolong Nature Reserve in the western margin of the Chengdu Plain (30°45'–31°25'N, 102°52'–103°24'E) is located in the upper reaches of the Minjiang River and the eastern slopes of the Qionglai mountains. The local climate shows attributes belonging to the Central Asian subtropical humid region, with annual average temperature of 8.4°C and rainfall of 861.8 mm. The distribution of the native vegetation exhibits significant differences by elevation in this mountain area (Administration Bureau of Wolong Nature Reserve, 1987).

Plot sampling was designed in the mountains around Wuyipeng field observation station, where the typical vegetation consists of thermophilic coniferous broad-leaved mixed forests and coniferous forests of *A. faxoniana*. The dominant species in the tree layer included coniferous species such as *A. faxoniana*, *Tsuga chinensis* and *Picea brachytyla* and broad-leaved species, such as *B. albo-sinensis* and *Acer tetramerum*. The undergrowth consisted often largely of *Gelidocalanus fangianus*, while *Fargebia rebugta* was restricted to the lower limits of our investigation range. In addition, *Rhododendron*, *Sorbus* and *Ribes* spp. as well as *Viburnum betulifolium* and *Rubus mesogaesus* were also well represented in the shrub layer. Relative to the flourishing shrub layer, sparse vegetation was found in the herb layer, with common species of *Cacalia* spp., *Ligularia* spp., *Lonicera microphylla*, *Smilacina henryi*, *Fragaria* spp. and *Oxalis griffithii*. However, the moss layer developed well, covering most of the earth with a thick green mantle. The interlayer gave priority to *Actinidia kolomikta* var. *Gagnepainii* and *Smilax menispermoides*.

---

## 3 Methods

We used a line transect method in our gap investigation. Three parallel sampling lines were selected along the mountain ridge, on sunny and on shady slopes respectively. Three types of gap features along each sampling line were recorded or calculated, i.e., gap shape features, gap regeneration features (including number and taxonomy of seedlings) and gap maker features (Table 1). Topographic indicators, such as elevation, slope and aspect, as well as topsoil samples for physical and chemical analysis, were also measured and collected during sampling of the communities.

The gap sizes were restricted from 4 to 1000 m<sup>2</sup>, for gaps less than 4 m<sup>2</sup> could not be distinguished from the space

among trees and areas larger than 1000 m<sup>2</sup> were equivalent to forest clearings, which are beyond the scope of small interference. The gap area was calculated by elliptical area formula,  $A = \pi LW/4$ , where  $L$  is the length of ellipse, and  $W$  the width of ellipse (Runkle, 1982).

The factors affecting gap regeneration could be divided into four types: soil properties, topography, gap makers and gap shape characteristics. From these, 15 environmental parameters were selected for principal component analysis. Data were standardized beforehand by the following formula:  $x'_i = [x_i - \min(x)] / [\max(x) - \min(x)]$ .

The dominance of seedlings (< 1.4 m tall) was depicted by [(relative abundance + relative frequency)/2] and that of gap makers by [(relative abundance + relative frequency + relatively prominence)/3]. Moreover, six biodiversity indices were calculated for analytical purposes using the following formulas.

$H'$  (Shannon-Wiener diversity index):

$$H' = \sum_{i=1}^s (P_i)(\ln P_i)$$

$MI$  (Margalef's index):  $MI = \frac{(s-1)}{\log_2 N}$

$J$  (evenness index):  $J = H'/H_{\max}(H_{\max} = \ln s)$

$C$  (Simpson's dominance):  $C = \sum_{i=1}^s (P_i)^2$

$TSR$  (transformed species richness):  $TSR = s/\ln(A)$  (Jiang et al., 2002)

$R$  (richness):  $R = s$

where  $s$  is the number of species,  $P_i$  the individual percentage of species  $i$ ,  $N$  the size of the population and  $A$  the size of sampling area.

## 4 Results and analysis

### 4.1 Distribution characteristics of gap interference

Gap interference and gap regeneration is often subjected to the same biophysical limits. Given a particular forest, the manner of gap formation and gap characteristics are often determined by the interaction between internal factors, such as the composition of species and age classes of the dominant tree layer and external factors, such as solar radiation, earth substrates and topography. As a forest gap develops, the local microenvironment changes, regardless of whether these are, suitable or unsuitable for the development of its dominant populations. In our investigation, it was found that topographic factors were significantly correlated with some characteristics of gap interference, given the total of 55 gaps encountered on the three sampling lines, as shown in Table 1.

Analyses show that those gap makers from tree cutting were positively and significantly correlated with the elevation gradient, while those formed by root pulling were positively and significantly correlated with the slope

**Table 1** Pearson correlations between gap interference characteristics and topographic factors

| gap interference characteristics | elevation | slope angle | aspect |
|----------------------------------|-----------|-------------|--------|
| gap size characteristics         |           |             |        |
| EG                               | 0.094     | -0.192      | 0.111  |
| CG                               | 0.050     | -0.083      | 0.167  |
| DH                               | 0.091     | -0.105      | 0.183  |
| gap maker characteristics        |           |             |        |
| GM <sub>n</sub>                  | -0.152    | 0.231       | 0.304* |
| SP <sub>n</sub>                  | -0.115    | 0.197       | 0.144  |
| S <sub>max</sub>                 | 0.156     | -0.153      | -0.182 |
| S <sub>tot</sub>                 | 0.122     | -0.122      | 0.023  |
| gap forming manners              |           |             |        |
| DM                               | -0.135    | 0.226       | 0.142  |
| KF                               | 0.297*    | -0.168      | 0.046  |
| GB                               | -0.236    | 0.295*      | 0.175  |
| ZG                               | -0.219    | -0.033      | 0.031  |
| KL                               | -0.011    | 0.153       | 0.186  |

Note: EG: area of expanded gap; CG: area of canopy gap; DH: ratio of gap diameter to gap height; GM<sub>n</sub>: number of gap makers; SP<sub>n</sub>: number of species of gap maker; S<sub>max</sub>: maximum basal area of gap makers; S<sub>tot</sub>: total area of gap makers; DM: number of tree falls; KF: tree cutting; GB: root pulling; ZG: trunk snapping; KL: standing dead. \*  $p < 0.05$  (2-tailed) ( $n = 55$ ).

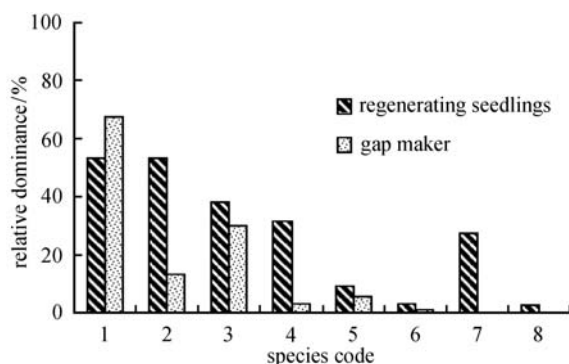
angle. Similar relationships were found between the number of gap makers before the gap occurred and the aspect. The gaps formed by human interference (history of tree cutting) seemed to be more prevalent on relative flat locations, such as ridgelines. This was confirmed by a significant, negative correlation ( $p < 0.05$ ) between elevation and slope, within the elevation range of the gap investigation from 2650 to 3000 m, which resulted in a significantly positive correlation between deforestation and elevation. The positive correlation between the gap formed by root pulling and slope angle was due to the greater prevalence of strong winds at locations with a steep gradient. In addition, we found in our survey more forest clearings and a larger number of pre gap makers at sunny slopes than at shady slopes, which may explain the positive correlation between the number of pre gap makers and aspect. The causes and effect of gap formation is discussed in an earlier study by Yang et al. (2004), who found that, topographic factors had partially contributed to the spatial differentiation and coalition of natural and human disturbances, which subsequently had an impact on gap regeneration patterns and characteristics.

### 4.2 Regeneration recruitment in forest gaps

#### 4.2.1 Species composition characteristics of gap makers and renewal seedlings

In the 55 gaps encountered on the sampling lines, the species composition of renewal seedlings was richer than

that of gap makers. We found eight species of regeneration seedlings and six species of gap makers, of which one species was represented by a relative dominance of just over 1%. The relative dominances are shown in Fig. 1. Seedlings denoted by relative dominance were sorted, showing that *Betula* spp. ranked the highest in species composition, followed in turn by *Abies faxoniana*, *Tsuga chinensis*, *Rhododendron* spp. and *Acer* spp., while the relative dominance of gap makers was concentrated in the leading species *Abies faxoniana* and *T. chinensis*. Since the seedlings belonging to *Betula* and *Rhododendron* could not be distinguished easily before maturity, they were classified into two large groups for statistical purposes.



**Fig. 1** Comparison of relative predominance between regenerating seedlings and gap makers. 1: *Abies faxoniana*; 2: *Betula* spp.; 3: *Tsuga chinensis*; 4: *Rhododendron* spp.; 5: *Picea brachytyla*; 6: *Prunus pilosiuscula*; 7: *Acer* spp.; 8: *Pinus armandi*.

#### 4.2.2 Spearman correlation analysis of regenerative seedlings in gaps

The recruitment distribution pattern reflects the response of seedlings to changes in the micro-environment after gap formation, i.e., the impacts of gap disturbance in between-habitat diversity. Based on the Spearman correlation analysis of the four dominant renewal seedling species, the results show a significant positive correlation between *A. faxoniana* and *T. chinensis* (Table 2). Correlations between pairs of other types of seedlings were not significant. However, the negative correlation between

**Table 2** Spearman correlation coefficients of between gap regenerating species

|                        | <i>Abies faxoniana</i> | <i>Tsuga chinensis</i> | <i>Rhododendron</i><br>spp. |
|------------------------|------------------------|------------------------|-----------------------------|
| <i>Betula</i> spp.     | 0.258                  | -0.089                 | -0.124                      |
| <i>Abies faxoniana</i> |                        | 0.292*                 | 0.056                       |
| <i>Tsuga chinensis</i> |                        |                        | 0.060                       |

Note: \*  $p < 0.05$  ( $n = 55$ ).

*Betula* and *Rhododendron* or between *Betula* and *T. chinensis* was due to a certain resource choice differentiation between these species in the regeneration phase.

#### 4.2.3 Relationships between the recruitment seedlings and gap regeneration setting

##### 1) Environmental factors for principal component analysis

In order to minimize the random effect of redundant data on the analysis, four categories of environmental factors relative to gap regeneration were selected for principal component analysis (PCA). The four categories and corresponding ingredients, denoted by  $C_1 - C_{15}$  were: 1) soil nutrient features:  $C_1$  nitrogen content (%),  $C_2$  organic matter content (%),  $C_3$  soil pH,  $C_4$  total phosphorus content ( $\mu\text{g/g}$ ),  $C_5$  total kalium content ( $\mu\text{g/g}$ ); 2) topographic features:  $C_6$  elevation (m),  $C_7$  slope ( $^\circ$ ),  $C_8$  aspect (divided into 8 classes based on light conditions); 3) characteristics of gap makers:  $C_9$  species richness,  $C_{10}$  total basal-area,  $C_{11}$  largest basal-area,  $C_{12}$  number of pre gap makers; 4) gap shape and size characteristics:  $C_{13}$  crown gap area,  $C_{14}$  expansive gap area and  $C_{15}$  the ratio of gap diameter to gap height. Given the cumulative percentage of eigenvalues over the 70% limit, only the first five principal components extracted from the correlation matrix were selected for further analysis (Table 3).

According to the load assignment distribution in Table 3, the largest contributions made to the five principal components were:  $C_{13}$ ,  $C_{14}$  and  $C_{15}$  to  $PC_1$ ,  $C_1$ ,  $C_2$  and

**Table 3** Eigenvalues extracted from correlation matrix

| variable              | $PC_1$ | $PC_2$ | $PC_3$ | $PC_4$ | $PC_5$ |
|-----------------------|--------|--------|--------|--------|--------|
| $C_1$                 | -0.128 | 0.506  | -0.070 | 0.168  | -0.152 |
| $C_2$                 | -0.177 | 0.507  | 0.032  | 0.210  | -0.123 |
| $C_3$                 | -0.099 | 0.250  | -0.173 | -0.209 | 0.535  |
| $C_4$                 | -0.155 | 0.453  | -0.111 | -0.227 | -0.220 |
| $C_5$                 | 0.091  | -0.234 | 0.065  | -0.431 | -0.147 |
| $C_6$                 | -0.026 | -0.078 | -0.452 | -0.183 | -0.477 |
| $C_7$                 | 0.053  | -0.001 | 0.542  | 0.233  | 0.134  |
| $C_8$                 | -0.126 | 0.076  | 0.418  | 0.085  | -0.151 |
| $C_9$                 | -0.187 | -0.057 | 0.286  | -0.262 | -0.371 |
| $C_{10}$              | -0.316 | -0.269 | -0.134 | 0.383  | -0.125 |
| $C_{11}$              | -0.158 | -0.207 | -0.273 | 0.529  | -0.097 |
| $C_{12}$              | -0.331 | -0.079 | 0.306  | -0.036 | -0.223 |
| $C_{13}$              | -0.468 | -0.059 | -0.033 | -0.097 | 0.287  |
| $C_{14}$              | -0.464 | -0.133 | -0.070 | -0.135 | 0.201  |
| $C_{15}$              | -0.432 | -0.080 | 0.022  | -0.166 | 0.042  |
| eigenvalue            | 3.546  | 2.795  | 2.287  | 1.471  | 1.032  |
| proportion            | 0.236  | 0.186  | 0.152  | 0.098  | 0.069  |
| cumulative proportion | 0.236  | 0.423  | 0.575  | 0.673  | 0.742  |

$C_4$  to  $PC_2$ ,  $C_6$ ,  $C_7$  and  $C_8$  to  $PC_3$ ,  $C_{11}$ ,  $C_5$ ,  $C_{10}$  and  $C_9$  to  $PC_4$ ;  $C_3$  and  $C_6$  to  $PC_5$ . Presumably, the first three principal components,  $PC_{1-3}$ , reflect gap shape and size features (CG, EG, DH), soil nutrient ingredients (total N, P, C content) and topographic factors (elevation, slope and aspect), respectively. The principal component  $PC_4$  is associated with characteristics of gap makers, i.e., species richness, total basal-area, largest basal-area (which indirectly reflects the gap disturbance intensity) and soil nutrients (total kalium content).  $PC_5$  mainly reflects the impacts of soil pH and elevation.

2) Correlation analysis on the abundances/biodiversity of renewal seedlings and gap regeneration setting

A Pearson correlation analysis explored the relationship between the abundance of major regenerating species in the gap and environmental principle components (Table 4), as well as between the biodiversity indices of renewal seedlings and principle components of the environment in the gap (Table 5).

**Table 4** Pearson correlations between the abundance of regenerative species and environmental principle components

| regenerative species     | PC <sub>1</sub> | PC <sub>2</sub> | PC <sub>3</sub> | PC <sub>4</sub> | PC <sub>5</sub> |
|--------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| <i>Betula</i> spp.       | -0.048          | -0.011          | -0.275*         | 0.010           | -0.048          |
| <i>Abies faxoniana</i>   | -0.111          | 0.563**         | -0.143          | -0.079          | -0.210          |
| <i>Tsuga chinensis</i>   | -0.024          | -0.056          | 0.093           | -0.020          | 0.121           |
| <i>Rhododendron</i> spp. | -0.048          | 0.196           | 0.351**         | 0.298*          | 0.025           |

Note: \*  $p < 0.05$ ; \*\*  $p < 0.01$  ( $n = 55$ ).

**Table 5** Pearson correlations between biodiversity indices of regenerative seedlings and environmental principle components

| biodiversity indices | PC <sub>1</sub> | PC <sub>2</sub> | PC <sub>3</sub> | PC <sub>4</sub> | PC <sub>5</sub> |
|----------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| $H'$                 | -0.075          | -0.271*         | -0.071          | 0.002           | 0.173           |
| MI                   | -0.101          | -0.055          | -0.077          | 0.089           | 0.329*          |
| $J$                  | 0.115           | -0.401*         | -0.054          | -0.265          | -0.028          |
| $C$                  | 0.004           | 0.328*          | -0.076          | 0.054           | -0.112          |
| TSR                  | 0.016           | 0.082           | 0.227           | 0.242           | 0.294*          |
| $R$                  | -0.188          | 0.054           | 0.172           | 0.176           | 0.290*          |

Note:  $H'$  is Shannon-Wiener diversity index; MI is Margalef's index;  $J$  is evenness index;  $C$  is Simpson's dominance; TSR is transformed species richness;  $R$  is richness;  $p < 0.05$  ( $n = 55$ ).

A significantly negative correlation was found between renewal seedlings of *Betula* and the third principal component, which suggests a large impact of topography on *Betula* regeneration. A significantly positive correlation between renewal seedlings of *A. faxoniana* and the second

principal component suggests the primary effect of soil nutrient on *A. faxoniana* regeneration. Similarly, significant positive correlations between *Rhododendron* spp. seedlings and the third and fourth principal components reflect the impacts of topographic factors and characteristics of gap makers on *Rhododendron* settlement. No significant correlation was found between *T. chinensis* seedlings and the five principal components mentioned earlier. The impacts of terrain on the regeneration of *Rhododendrons* and *Betula* were opposite which resulted in the spatial separation of the distribution of their seedlings.

It is shown in Table 5 that  $H'$  (Shannon-Wiener diversity index),  $J$  (evenness index) and  $C$  (Simpson's dominance) were significantly correlated with the second principal component, which reflects a great impact of soil nutrients on these indices. Moreover,  $C$  was positively correlated with  $PC_2$ , while  $J$  and  $H'$  were negatively correlated with  $PC_2$ .  $MI$ ,  $TSR$  and  $R$  were positively correlated with  $PC_5$  which also partially reflects the impact of the soil pH. Thus, the biodiversity of renewal seedlings was largely affected by soil properties.

## 5 Discussion

It could be inferred from the contrast of composition and relative predominance between renewal seedlings and gap makers that broad-leaved species, such as *Betula*, *Acer* and *Rhododendron* and not conifer species, especially not *A. faxoniana*, were strongly dominant in the natural recruitment of seedlings. In the western mountainous area of Sichuan, the regeneration of most *A. faxoniana* populations is in poor shape. Over maturity, low fecundity, thick ground cover and low soil temperature have taken an enormous toll in their effects on their natural regeneration (Sichuan Vegetation Collaborative Group, 1980). Contrarily *Betula* populations were able to take advantage of their high fecundity, large seed pools, strong seed vitality and invasive capacity of seeds. Their natural regeneration is quite good. Presumably, forest communities in our study area are still in an unstable phase of a series of successions. Some important local habitats of dominant species were easily replaced by *Betula*, *Rhododendron* or *Gelidocalanus fangianus* shrubs. Accordingly, the physiologic mechanism on the natural recovery of *A. faxoniana* populations must be further explored. Moreover, proper artificial supplementary measures to improve the regenerating microenvironments to strengthen their seedling predominance are strongly recommended.

Taylor and Qin (1988) speculated that in this area *A. faxoniana* and *B. utilis* seem to regenerate frequently in gaps of different sizes and gap partitioning by size may be contributing to their coexistence. As a good colonist, *Betula* tends to regenerate most frequently in large gaps of

temperate forests. It was confirmed in our survey that the cleared forest areas were most frequently filled by *Betula*. But in terms of gap interference (crown gap size less than 1000 m<sup>2</sup>), the competitive advantage of *Betula* was maintained; their seedlings headed the list of relative predominance. Thus, relative to other factors (such as soil nutrients, local terrain and intensity of gap interference, etc.), gap size was no longer the crucial determinant for spatial regeneration patterns. In addition, neither the abundance of each dominant regenerating species nor their biodiversity indices had shown significant correlation with the first principal component of environmental gap factors, which also indicated that characteristics of gap size had not made any notable impact on gap regeneration patterns. In contrast, we speculated that soil properties were the crucial factors affecting gap regeneration, for they had shown, until now, significant impact on both seedlings of *A. faxoniana* and on species diversity. However, the influencing mechanism of soil properties on regenerating seedlings and how it functions has, up until now, remained unclear.

**Acknowledgments** This research was funded by the National “973” Key Basic Research Projects (Nos. G2000046802 and 2002CB111507) and the National Natural Science Foundation of China (Grant No. 30270254). The field investigation was supported and assisted by the Giant Panda Research Center in Wolong Natural Reserve and the Life Science College of Southwest China University, for which we are grateful.

## References

- Administration Bureau of Wolong Nature Reserve (1987). Vegetation and Plant Resources of Wolong. Chengdu: Sichuan Science & Technology Publishing House (in Chinese)
- Brokaw N V L (1985). Gap-phase regeneration in a tropical forest. *Ecology*, 66: 682–687
- Duke N C (2001). Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. *Wetlands Ecol Manag*, 9: 257–269
- Jiang M X, Deng H B, Tang T, Cai Q H (2002). On spatial pattern of species richness in plant communities along riparian zone in Xiangxi River watershed. *Acta Ecol Sin*, 22:629–635 (in Chinese)
- Luo D Q, Guo Q S, Xue H Y, Bian B D J (2002). Characteristics and disturbance status of gaps in subalpine fir forest in Southeast Tibet. *Chin J App Ecol*, 13: 777–780 (in Chinese)
- Rebertus A J, Burns B R (1997). The importance of gap processes in the development and maintenance of oak savannas and dry forest. *J Ecol*, 85: 635–645
- Runkle J R (1982). Pattern of disturbance in some old-growth mesic forest of eastern North American. *Ecology*, 62: 1041–1051
- Runkle J R (1985). Comparison of methods for determining fraction of land area in tree-fall gaps. *For Sci*, 31: 15–19
- Schupp E W (1989). Arrival and survival in tropical tree fall gaps. *Ecology*, 70: 562–564
- Shao G F, Zhao S D, Shugart H (1989). Forest Dynamics Modeling: Preliminary Explanations of Optimizing Management for Korean Pine Forests. Beijing: China Forestry Publishing House (in Chinese)
- Shen Z H, Li D X, Wang G F (2001). Studies on the gap disturbance of the mountain mixed forests of evergreen and deciduous broad-leaved species at MT. Dalaolin in the Three Gorges I. The essential characteristics of the gaps. *Acta Phytoecol Sin*, 25: 276–282 (in Chinese)
- Sichuan Vegetation Collaborative Group (1980). Sichuan Vegetation. Chengdu: Sichuan People’s Publishing House (in Chinese)
- Spies T A, Franklin J F (1989). Gap characteristics and vegetation responses in coniferous forests of the Pacific Northwest. *Ecology*, 70: 543–545
- Taylor A H, Qin Z S (1988). Regeneration patterns in old-growth *Abies-Betula* forest in Wolong natural Reserve Sichuan, China. *J Ecol*, 76: 1024–1218
- Veblen T T (1992). Regeneration dynamics. In: Glennlewin D C. ed. Plant Succession: Theory and Prediction. London: Chapman & Hall, 152–177
- Wang Z P, Li X G, Shi S Y, Qi D H, He Z M, Xu W W, Deng X B (2003). A comparison study on the species diversity between the gap and non-gap in Jinyun Mountain. *Chin J App Ecol*, 14: 7–10 (in Chinese)
- Wu G, Yin R B, Zhou Y B, Hao Z Q, Lang X Y (1999). The influence of gap regeneration dynamics to early-spring herb in the Korean pine broad-leaved forests in Changbai Mountain. *Acta Ecol Sin*, 19: 659–663 (in Chinese)
- Wu N (1999). Dynamics of forest gaps in subalpine coniferous forests on the eastern slope of Gongga Mountain. *Acta Phytoecol Sin*, 23: 228–237 (in Chinese)
- Yang J, Liu L J, Ge J P, Ding Y, Tan Y C (2004). Characteristics of canopy gap disturbance in Wolong Nature Reserve. *Acta Phytoecol Sin*, 28: 723–726 (in Chinese)
- Yang X (2002). Gap characteristics and disturbance regime in a dark coniferous forest in Changbai Mountain areas. *Acta Ecol Sin*, 22: 1845–1831 (in Chinese)
- Yu Z L, Zhao S D (1997). Advances of gap model. *Chin J Ecol*, 16(2): 42–46 (in Chinese)
- Zang R G, Liu J Y, Dong D F (1999a). Gap Dynamics and Forest Biodiversity. Beijing: China Forestry Publishing House (in Chinese)
- Zang R G, Yu S X, Liu J Y, Yang Y C (1999b). The gap phase regeneration in a tropical montane rain forest in Bawangling, Hainan Island. *Acta Ecol Sin*, 19: 151–158 (in Chinese)