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# Spatial variation of seed rain and seed banks in gaps of karst forest in the Maolan Nature Reserve, Guizhou Province

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**Abstract** Based on an investigation on gaps and non-gap stands of the Maolan National Karst Forest Nature Reserve, Guizhou Province, quantitative characteristics and dynamic changes of seed rain and seed banks in gaps were analyzed. The results show that the total amount of seed rain was  $117.4 \pm 32.6$  seeds/m<sup>2</sup> during the period of observation. The number of immature seeds was  $56.3 \pm 10.3$  seeds/m<sup>2</sup>, that of mature damaged seeds was  $15.7 \pm 4.7$  seeds/m<sup>2</sup>, and the number of mature germinated seeds was  $45.4 \pm 8.2$  seeds/m<sup>2</sup>. It is suggested that the seed number is rich for gap regeneration. Seed rain in gaps has spatial and temporal heterogeneities which deeply affect regeneration patterns of gap plants. Along a gradient from the gap center to a non-gap stand, seed density in the litter layer, the number of species, and the Shannon-Wiener diversity index were gradually reduced, but these indices increased in the soil. The seed density in the gap center was  $2415 \pm 639$  seeds/m<sup>2</sup>, near the gap center was  $2218 \pm 421$  seeds/m<sup>2</sup> and at the gap border area  $1815 \pm 311$  seeds/m<sup>2</sup>. This shows that plants in gaps have good latent regeneration potential. In both gaps and non-gap stands, the Jaccard similarity index of seed in litter layer was the largest, second largest at 5–10 cm soil depth, and the least at the 0–5 cm soil layer the index. The Jaccard index between the soil seed bank and the present plant community was large in the litter layer, but decreased with soil depth both in gaps and non-gap stands. The results show that soil seed banks are the main source of gap regeneration in the karst forests of Maolan and contribute significantly to gap regeneration.

**Keywords** karst forest, gap, seed rain, seed bank, Maolan

Translated from *Acta Botanica Yunnanica*, 2007, 29(3): 327–332 [译自: 云南植物研究]

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## 1 Introduction

The soil seed bank is an important component in vegetation regeneration ability (Zhang, 1996). It is related to succession and development of plant communities and is also closely related to vegetation dynamics. The relationship between seed rain, soil seed bank and ground vegetation has become one of the more intensively studied areas in modern ecology (Young et al., 1987; Wang and Liang, 1995; Ban and Xu, 1996). During the period of gap regeneration, aside from the growth of seedlings and saplings and the early regeneration and re-sprouting of damaged trees, the germination of seeds in original soil banks and seed dissemination into gaps are important additional ways to fill the gap (Jones et al., 1994). Factors such as gap size, gap forming season (Canham et al., 1990) and gap age (Whitmore, 1989) have an intense effect on seed dissemination and microclimate in gaps, and they exert direct effects on the renewal conditions in gaps and the differences between forest structures in gap and non-gap stands. Therefore, to investigate the dynamic changes of seed release and seed banks in gaps is of vital importance to reveal the pattern and process of forest regeneration. Studies of seed rain and seed banks in gaps are few and far between (Denslow and Diaz, 1990; Chandrashekara and Ramakrishnan, 1993). Up to now, there have been no published reports in China on this subject. Therefore, we have analyzed the quantitative attributes and dynamic rules governing seed rain and seed banks in gaps to reveal latent regeneration and patterns and processes of regeneration in karst forests in order to provide a reference for karst forest management and its operations.

## 2 Study area

This study was conducted in the Maolan National Karst Forest Nature Reserve (20000 hm<sup>2</sup>; 25°09′–25°20′N, 107°52′–108°05′E; elevation 850 m), Libo County, Guizhou Province in southwestern China. The karst geomorphology is mainly composed of pure limestone and

dolomite rocks (well-developed funnels and lowlands among peaks). Based on its sparse distribution pattern, it belongs to the karst outcrop type, called the “typical karst habitat”. This karst geomorphology, together with forests growing on the base rocks in this habitat, form a unique natural complex of karst forests in the subtropical region. The meteorological features in the Maolan karst area are as follows: solar radiation is  $907 \times 10^5 \text{ Ca}/(\text{cm}^2 \cdot \text{year})$ , the annual mean temperature is  $15.3^\circ\text{C}$ , the mean annual difference between high and low temperatures is  $18.3^\circ\text{C}$ , the actively accumulated temperature is  $4598.6^\circ\text{C}$ , annual precipitation is at  $1752.5 \text{ mm}$ , and the mean annual relative humidity is 83%. The limestone soil in the Maolan karst forest has poor water-holding capacity but is rich in organic matter and micronutrients (N, P, K) and alkali.

The karst geomorphology has unique ecological features. These features exert a tremendous effect on the development of the soils and forests. The Maolan karst forest is a mixed evergreen and deciduous broadleaved forest. It has non-zonal vegetation, a kind of steady climax community of soil and topography which develops under the conditions of a mid-subtropical moist climate, and is affected by some special habitats such as karst geomorphology, limestone soil, etc. The common broad-leaved trees are *Cyclobalanopsis glauca*, *Quercus phillyraeoides*, *Lindera comunis*, *Platycarpus longipes*, *Pistacia chinensis*, *Boniioderon minus*, *Chandeliodendron bodimieri*, *Chaerospondias axillaries*, *Viburnum*, *Photinia glabxa*, *Manglietia calcarea*, *Cladrastis platycarya*, *Machilus rehderi*, *Clausena dumni-ana*, *Sapium rotundifolium*, *Acer cinnamomifolium*, *Cinnamomum wilsonii*, etc. The shrub layer consists of *Mahonia confusa*, *Nandian domestica*, *Aucuba spp.*, *Ampelocalamus calcareous*, *Dendrocalamus tsaigii*, etc. The herb layer consists of *Elatostema stewardii*, *Selaginella uncinata*, *Bryophyta*, *Pyrrosia lingua*, *Carex sp.*, *Asparagus cochinchinensis*, *Cyrtogonellum fraxinellum*, etc. These dense virgin forests in the subtropics developed into landscapes of funnel, depression and basin forests, which are currently rarely seen in areas on the same latitude in China or even in the world, and maintain a typical pattern of virgin forest ecosystems.

### 3 Methods

We selected four gaps in the same landform position with stand ages of about five years old. Each gap area had an expanse of  $100 \text{ m}^2$ . The gaps were all formed by natural processes. In each gap, all trees were measured for diameter at breast height (DBH) (1.3 m above the ground), and height, crown and species were identified. All saplings (1 m tall and  $<5 \text{ cm}$  DBH) and seedlings ( $<1 \text{ m}$  tall, including one year seedlings) were enumerated by species.

Density was estimated by counting; herbs were recorded by species, and abundance was estimated in four subplots each with an area of  $1 \text{ m} \times 1 \text{ m}$ , spaced evenly in the four corners of each gap. Nine  $1 \text{ m}^2$  seed collection frames were placed in the center of the gap, near the center and at gap borders in the four cardinal directions of each gap (Fig. 1). There was a total of 36 seed collection frames in the four gaps. Each frame was fixed at a height of 50 cm above the ground. Litter in the seed collection frame was collected every 10 days from August 1 to late February. The species and number of seeds were recorded with an experimental germination method. We stipulated that the seeds which germinated in our germination experiment were mature seeds; seed which looked mature but suffered injury and were not germinating were declared mature damaged seeds; seeds with their shape intact but small and not germinating were immature seeds (Liu and Zhong, 2000). At the beginning of natural germination (late February) in the seed bank, litter in the  $50 \text{ cm} \times 50 \text{ cm}$  collection area beside the seed collection frame in the closed forest was collected. Soil samples of  $10 \text{ cm} \times 10 \text{ cm}$  sizes at depths of 0 to 5 cm and 5 to 10 cm under the collected litter were gathered, as well as three soil samples and litter in non-gap stands. There were altogether 36 soil samples in four non-gap stands. The soil and litter samples were placed under suitable conditions for seeds to sprout. Soil moisture was maintained until seedlings appeared.

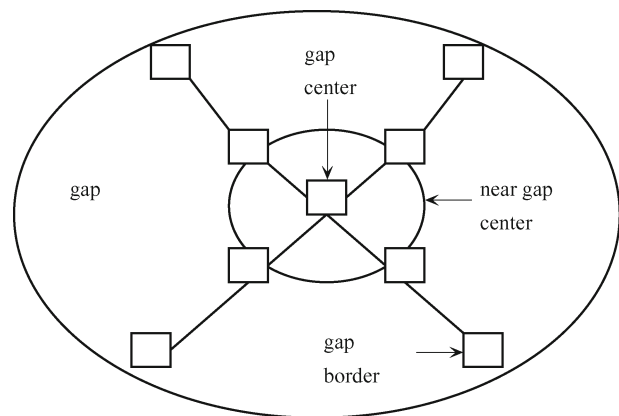


Fig. 1 Placement of seed rain collection frames in one gap of the karst forest

We selected the Jaccard similarity index ( $C_j$ ) (Whittaker, 1972) to calculate the similarity of soil seed banks between gap and non-gap stands. The index is stated as follows:

$$C_j = c / (a + b - c) \quad (1)$$

where  $c$  is a common species in soil seed bank of gaps and non-gap stands,  $b$  the number of species in the soil seed bank in gaps, and  $a$  the number of species in the soil seed bank in non-gap stands.

## 4 Results

### 4.1 Characteristics of seed release in gaps

#### 4.1.1 Species and quantity of seed release

During our period of observation, the amount of seed rain was  $117.4 \pm 32.6$  seeds/m<sup>2</sup>, in which the number of immature seeds was the largest, reaching  $56.3 \pm 10.3$  seeds/m<sup>2</sup>, and accounted for 48.0% of all released seeds; the number of damaged mature seeds was  $15.7 \pm 4.7$  seeds/m<sup>2</sup>, accounting for 13.4%; and, the number of germinated mature seeds was  $45.4 \pm 8.2$  seeds/m<sup>2</sup>, accounting for 38.7% (Table 1). It can therefore be seen that, for some reasons, a massive amount of seeds had fallen before maturing in the course of gap regeneration. Among the mature seeds, there were some seeds damaged by animals or eaten by insects, which led the greater loss of seed. The amount of mature seeds, i.e., 45.4 seeds/m<sup>2</sup>, was quite adequate for plant community regeneration. The amount of seeds originating in the gap for gap regeneration was quite enough if the number of immature seeds during the observation period were added. These numbers provide evidence that the cycling rate of the soil seed bank in the gap was very high. There were ten tree species releasing seed in the gap, including seven tree species which altogether produced 78.2 seeds/m<sup>2</sup> and accounted for 67% of the total amount of seed rain. The number of immature seeds was 33.3 seeds/m<sup>2</sup>, the number of mature damaged seeds was 10.6 seeds/m<sup>2</sup> and that of germinated mature seeds was 34.3 seeds/m<sup>2</sup>. These number of seeds accounted, respectively, for 59.1%, 67.5% and 75.6% of the all the seeds released. The amount of seeds of shrubs such as *Euonymus dielsianus*, *Viburnum propinquum* and *Rhamnus globosa* accounted for the 33.4% of the total seed rain, of which 11.1 seeds/m<sup>2</sup> were mature germinated seeds and accounted for 24.4% of the total number of mature germinated seeds released. It should be pointed out that, from the species composition of the seed rain in the gap, the number of seeds of dominant trees and shrub species

**Table 1** Composition and structure of seed rain in gaps (unit: seeds·m<sup>-2</sup>)

species	immature seeds	mature germinated seeds	mature damaged seeds	total
<i>Cladrastis platycarpa</i>	0.8	4.4	1.6	6.8
<i>Symplocos adenophylla</i>	22.8	10.9	0.7	34.4
<i>Sapium rotundifolium</i>	1.3	0.5	0.1	1.9
<i>Euonymus dielsianus</i>	2.3	1.1	0.3	3.7
<i>Viburnum propinquum</i>	15.3	8.4	2.9	26.6
<i>Platycarya longipes</i>	0.3	16.9	4.6	21.8
<i>Gomphandra tetrandra</i>	4.2	0.6	0.3	5.1
<i>Poliothyrsis sinensis</i>	0.2	0.1	0.4	0.7
<i>Rhamnus globosa</i>	5.4	1.6	1.9	8.9
<i>Cyclobalanopsis myrsinaefolia</i>	3.7	0.9	2.9	7.5
total	56.3	45.4	15.7	117.4

in the community to enter the gap was quite high, which shows potential to provide a basis for plant renewal in the gap and maintain community stability.

#### 4.1.2 Spatial and temporal heterogeneity of seed rain in gaps

The amounts of seed rain at the gap center, near the center, and at the cardinal points of the gap border show statistically significant differences ( $p < 0.05$ ). The amounts of seed rain in the southern and western edges of the gap were large, and amounted to  $42.4 \pm 14.3$  seeds/m<sup>2</sup> and  $30.6 \pm 11.8$  seeds/m<sup>2</sup>, respectively. The amount of seed rain at the eastern edge was  $24.1 \pm 8.8$  seeds/m<sup>2</sup>, and at the northern edge was  $20.3 \pm 7.2$  seeds/m<sup>2</sup>, far less than at the other edges. The amount of seed rain at the center of the gap was  $46.8 \pm 17.4$  seeds/m<sup>2</sup>, at the gap border was  $39.2 \pm 11.5$  seeds/m<sup>2</sup> and near the center of the gap was  $31.4 \pm 9.1$  seeds/m<sup>2</sup>. The amounts of seed rain in the different directions and areas in the gap varied because mother trees are located in a non-uniform fashion and, combined with the action of thermodynamic cycles in the gap, resulted in a seed dispersion mechanism of different tree species which distributed seed in a manner far from random allocation. It also showed that the amounts of seed released at different times of observation were significantly different ( $p < 0.05$ ), given that we collected seeds at 21 different times. Seed dispersion in the gap had two peaks in late September and late October, and the number of seeds accounted for 25% and 36% of the total seed rain at these two times of observation. The amount of seed rain in late November was the second largest and accounted for 21%. The amount of seed rain before September was only 12% of the total amount of seed rain, and after December, only 6%. This shows that the release of seeds into the gap is not synchronized. We may conclude that seed input into the gap has both spatial and temporal heterogeneous characteristics. Further, the quality of seeds is different in both a spatial and temporal sense, which will have a profound effect on the renewal pattern of plants in the gap.

### 4.2 Characteristics of soil seed banks in gaps

#### 4.2.1 Quantitative attributes of soil seed banks

In a horizontal gradient from the gap center passing through the near gap center and the gap border to the non-gap stands, density, species abundance and species diversity of seeds in the soil layer (0–10 cm) and litter layer obeyed certain rules of change (Fig. 2). Seed density, number of species and the Shannon-Wiener diversity index decreased along the gradient from gap center to non-gap stands, but in the soil layer, the opposite change was observed. The seed density of the soil seed bank was  $2415 \pm 639$  seeds/m<sup>2</sup> at the gap center,  $2218 \pm 421$  seeds/m<sup>2</sup> near the gap center and

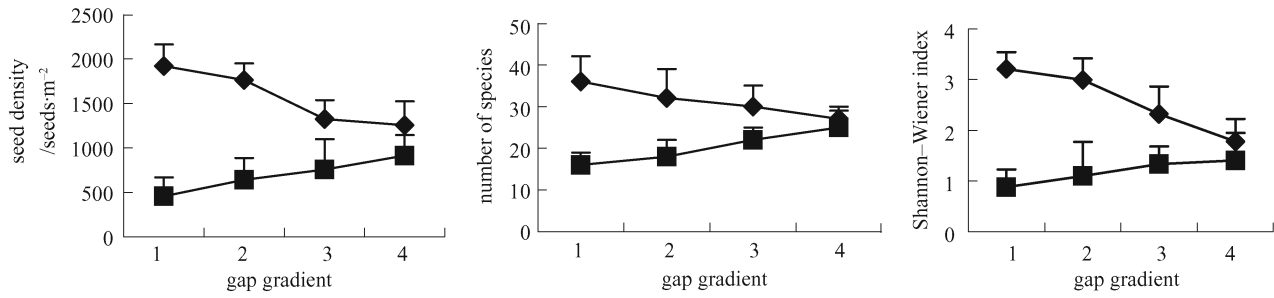


Fig. 2 Change of soil seed bank in gap gradient

1815 ± 311 seeds/m<sup>2</sup> at the gap border. It should be pointed out that the seeds in the different gap areas were extremely vigorous. The plants in the gap, therefore, have excellent regeneration potential. The difference in the vigor of the seeds of the soil seed bank in the various areas of the gap was the basic reason for regeneration density differences.

4.2.2 Analysis of soil seed bank between gap and non-gap stand showing similar trends

Between gap and non-gap stands, the Jaccard similarity coefficient of seeds in the litter layer was the highest at 0.2124, in the soil layer (5–10 cm) the second highest at 0.1861, and lowest in the 0 to 5 cm soil layer at 0.1447. It should be pointed out that the Jaccard similarity coefficient of the soil seed bank between gap and non-gap stands was low in the 0 to 5 cm soil layer but was high in the deep soil layer and in the litter layer. A possible reason is that seed in the litter layer in both gaps and non-gap stands originated from the existing vegetation, so the similarity was high. Seeds in the 5 to 10 cm soil layer were little affected by gap formation. The seeds had been accumulated over a long period of time during the vegetation growth process and the similarity was also high. The seed similarity at the soil surface layer (0–5 cm) was lowest between the gap and non-gap stands because the number of seeds at the soil surface of the gap was reduced after massive germination. It should be mentioned that because of improved light conditions in the gap to stimulate germination of the seeds at the soil surface, there was a great difference in species in the soil seed bank between gaps and non-gaps stands.

4.2.3 Similarity analysis between soil seed bank and surviving vegetation

There are certain connections between the soil seed bank and the surviving plant community because seeds produced by surviving species in the community enter the seed bank continuously. However, the seeds did not come entirely from the surviving community. Some differences do exist between the soil seed bank and the surviving community. The Jaccard seed similarity coefficient between soil seed and the surviving vegetation in the litter

layer was 0.1254, in the 0–5 cm soil layer was 0.0857, and in the deeper 5–10 cm soil layer was 0.0521 (Table 2). The Jaccard seed similarity coefficient in the corresponding layers between the soil seed bank and the surviving community in the non-gap stands was 0.3368, 0.0472 and 0.0263, respectively. Thus, it indicated that similarity between the litter layer and the surviving species in the community was the highest in both gaps and non-gap stands and decreased with increasing soil depth. The similarity was high between the soil seed bank in the gap and the surviving community, which indicated that seeds for gap regeneration mainly originated from the soil seed bank. The soil seed bank contributed much to the gap filling and plant regeneration.

Table 2 Jaccard indices between soil seed bank and present community of gaps and non-gap stands

layer	gaps	non-gap stands
litter layer	0.1254	0.3368
0–5 cm soil	0.0857	0.0472
5–10 cm soil	0.0521	0.0263

5 Discussion

Regeneration refers to the continuous process that plant species or a community undergoes from mature seed, falling into soil to germinate, and finally growing into vigorous and healthy plants or trees, growing with the original reservoir of tree species. It is also an essential step in the formation of multi-layered structures and multi-species composition of natural communities (Howard and Goldberg, 2001). Regeneration includes a series of complex stages. In the first stage, there is fertility, seed production and proliferation; in the second stage, seed germinates and matures after the seed falls to the ground or after a period of dormancy; in the third stage, seedlings mature; in the fourth stage, seedlings develop into saplings and finally mature as trees. At each stage, mutual relations exist and effects occur. Successful conditions for regeneration are as follows: there must be a reliable, original seed source; there must be suitable seed beds for seed germination and a suitable environment for seeds to germinate

and for seedlings to survive. Light condition is improved with the formation of gaps. Light is an important promoter for the germination of seeds in the gap. Gap regeneration is one of the important conditions for forest regeneration and is also the basis for sustainable development and the maintenance of a dynamic and stable natural forest. Therefore, during the process of gap regeneration, the release of seed, soil seed bank formation, seed sprouting and seedling growth are major steps and important constituents for a dynamic forest cycle. The study of these questions is of interest to reveal the intrinsic mechanism of the maintenance of species diversity in forests.

The main role of gaps in forest renewal is their effect on the invasion and establishment of plants. It is an important aspect affecting the change in species diversity in gaps and is exerted by species invasion into the gap. At first, seed sources and the amount of seeds will be severely affected by special environmental conditions in the gap. Meanwhile, heterogeneity of the microenvironment in the gap has a selective function in seed survival, seed germination and seedling establishment. Mutual actions between gap and seed characteristics or seedling shade tolerance, as well as between biotic and abiotic factors will affect the action of tree seeds arriving or surviving in gaps and growing to maturity, and ultimately affect the regeneration level of the forest. Secondly, the dynamic change of habitat resources (light and soil conditions) in the gap may also cause the species components to change during the process of gap growth (Hubbel and Foster, 1986), especially in the karst forest ecosystem where microenvironment types are diverse, the combinations, form and distribution patterns are complex, and spatial and temporal patterns of habitat resources have a very complicated effect on plant growth. The differences in seedling sources and habitat characteristics are the factors that facilitate species continuity and stability in the gaps of the Maolan karst forest. It can also explain why spatial variation of seed rain, type of seed bank and the amount of seeds are important. The proposition of which species can form, invade and settle down successfully, and of which species will be preserved, reduced or exterminated, involves the question of how species diversity of a community is restored and maintained. The explanation and hypothetical concerns of this aspect are quite considerable and invoke resource partitioning theory, competitive equivalence and competitive exclusion theory, etc. (Steege and Hammond, 2001). From the results of our quantitative study on the attributes of seed rain and soil seed banks of gaps in the Maolan karst forest, the amount of seeds released into gaps is extremely large and may provide enough source for seedling regeneration in the gaps. The amount of seeds buried in the soil seed bank of the gap was also large, which indicates that gap regeneration potential is great and can maintain the stability of the community. The results reported on sprout dynamics of soil seed banks in the wet tropical forest in Canada

studied by Chandrashekara and Ramakrishnan (1993) showed that gap source for regeneration mainly originates from soil seed banks, and the effect of external species in gap regeneration was minimal. These findings indicate that seed dispersion and soil seed bank formation in gaps is an important step for forest circulation and regeneration and is also an important mechanism of species diversity maintenance in the karst forest.

The abundance of seed rain has spatial and temporal heterogeneity which affects the amount and distribution pattern of seeds released from the soil seed bank in the gap. The combined action of the random distribution of the seed sources and the particular environment in the gap have caused a specific pattern of soil seed bank distribution, thus this will have an important effect on regeneration dynamics of future plant populations. The results studied about seed density, species abundance and species diversity of the soil seed bank along the horizontal gradient from the gap center, near gap center, gap border, to non-gap stands showed that seed density, species number and the Shannon-Wiener diversity index of seeds in the litter layer from the gap center to non-gap stands decreased, but changes in seed distribution in the soil showed an opposite trend. A possible reason is that light in the gap center is strong and the seed is not moist and will not easily rot like the seed in non-gap stands. At the same time, vegetation above the gap center is sparse, which increases the opportunity for seeds to fall into the gap. Therefore, the seed density of the litter layer in the gap center was high and decreased gradually along the gap border. The reason for low seed density in the soil at the gap center is possibly because the soil seed sprouted massively and was stimulated by improved light conditions during the initial period of gap formation. The changing light conditions observed along the horizontal gradient in the gap indicated that light intensity was reduced from the gap center to the closed forest, and the change in the amount of soil seeds assumed the same tendency. This indicates certain advantages for plant seed germination in gap formations and for the regeneration cycle in the karst forests. The tendency of the Jaccard seed similarity coefficient to change between gap and non-gap stands showed that it was low in the 0–5 cm soil layer but high at the litter layer and in the deep soil layer. This indicates that dynamic circulation exists not only in the surviving ground vegetation with gap regeneration, but also in the dormant seed population of the soil seed bank in the karst forest ecosystem. The change in the latent population (seed flows) is the basis for the existing dynamic circulation of the vegetation. According to a study of dynamic change patterns of soil seed banks and seedlings in brush vegetation in Tiantong Mountain, Zhejiang Province by Zhang (2001), we propose that the dynamic circulation process of the soil seed banks and seedlings could be summarized schematically (Fig. 3). In the vegetation growth process, seeds accumulate gradually in the soil, while seeds with a long life span are

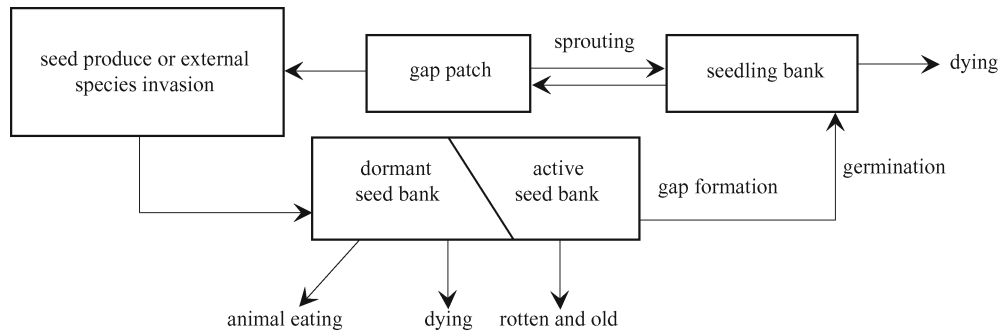


Fig. 3 Dynamic model of soil seed bank and its seedling bank in gaps of the Maolan karst forest

preserved in the soil seed bank as a result of an accumulation over time. When the seeds sprout and supplement the existing community, they form a seedling bank when light conditions are improved within a gap. The seedlings then grow gradually to the adult stage to form a new gap under the influence of various interferences and complete the dynamic circulation process of forest vegetation.

## 6 Conclusions

Species diversity maintenance by gaps in the forest is the result of two functional processes. 1) Time accumulation effect. Certain species entering the gap to establish their communities need enough time to complete the dispersion and establishment process successfully from their seed source to the multiple spatial targets, and the speed of this process directly affects the progress of species diversity restoration in gaps. Unquestionably, more and more species will complete this ecological process to form a species composition in the gap over time, i.e., it will complete the transformation process from seed release to seed bank. The speed of this process is decided by ecological factors such as size of the gap, ecological characteristics of species, distance of seed source, etc. 2) Evolution of community environment. Under mutual community and environmental functions after seedlings are established in the gap, continuous changes in the overall environment in the gap provides the possibility for greater species survival and multiplication. At the same time, different environments are possibly suitable for some species but not for other species. In addition, biological processes (mutual inter-species effect) also affect species diversity of the community and cause the number of species to change continuously at different times in the gap. This will have an important effect on the pattern and process of forest regeneration. Therefore, factors such as size and age of the gap, distribution patterns, and others affecting the amount of seed rain, seed bank and the dynamic change of the seedling bank should be studied further.

**Acknowledgements** We express our thanks to Zhibin XIONG and Luming WEI from the Management Department of the Maolan

National Nature Reserve in Guizhou Province, who took part in the field survey. This research was funded by the Natural Science Foundation of Guizhou Education Department (Guizhou Education-Science (2001028) and the Doctoral Fund of Guizhou Normal University.

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