

# Seed rain, soil seed bank, seed loss and regeneration of *Castanopsis fargesii* (Fagaceae) in a subtropical evergreen broad-leaved forest

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## Abstract

Understanding the seed rain and seed loss dynamics in the natural condition has important significance for revealing the natural regeneration mechanisms. We conducted a 3-year field observation on seed rain, seed loss and natural regeneration of *Castanopsis fargesii* Franch., a dominant tree species in evergreen broad-leaved forests in Dujiangyan, southwestern China. The results showed that: (1) there were marked differences in (mature) seed production between mast (733,700 seeds in 2001) and regular (51,200 and 195,600 seeds in 2002 and 2003, respectively) years for *C. fargesii*. (2) Most seeds were dispersed in leaf litter, humus and 0–2 cm depth soil in seed bank. (3) Frequency distributions of both DBH and height indicated that *C. fargesii* had a relatively stable population. (4) Seed rain, seed ground density, seed loss, and leaf fall were highly dynamic and certain quantity of seeds were preserved on the ground for a prolonged time due to predator satiation in both the mast and regular years so that the continuous presence of seed bank and seedling recruitments *in situ* became possible. Both longer time observations and manipulative experiments should be carried out to better understand the roles of seed dispersal and regeneration process in the ecosystem performance.

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**Keywords:** Mast seeding; Predator satiation; Seed bank; Subtropical evergreen broad-leaved forest

## 1. Introduction

The natural regeneration of plants is an important subject in both conservation biology and management (Guariguata and Pinard, 1998). Regeneration involves several stages of plant life cycles, i.e. seed production and seedling or sapling establishment and survival. Seed dispersal links the end of the reproductive cycle of adult plants with the establishment of their offspring, and has profound effects on vegetation structure. Confirming and quantifying such effects, however, have proven to be a challenge (Wang and Smith, 2002). The stages of seeds (e.g. seed dispersal or seed bank) and seedlings (or saplings) have been recognized as the most important stages in natural regeneration. In the past, seed banks, determined by dispersal, predation, preservation, and germination, have been considered as a major force governing the regeneration, structure, and succession of vegetation (Howe

and Smallwood, 1982; Kalin et al., 1999; Curran and Leighton, 2000; Fenner, 2000; Fuentes, 2002; Wenny, 2000; Dalling et al., 2002). Therefore, information on natural loss dynamics of seeds is critical for understanding the natural regeneration mechanisms of the focal species. Seed loss is another important process in studying seed banks and species regeneration. Early studies have adopted two major approaches: (1) observing the dynamics of seeds on the ground (or “natural” method; e.g. Shaw, 1968), and (2) “seed-collection, putting, and number-checking” (or “artificial method”; e.g. Hughes and Westorby, 1990; Whelan et al., 1991; Wang et al., 1999; Wang and Ma, 1999, 2001; Wenny, 2000; Schnurr et al., 2002). However, the latter has several practical limitations. First, it cannot accurately measure seed loss in natural conditions because the measuring time needed is usually not the period of seed fall. Second, predator activities and hunger level are not the same as those during seed fall. Finally, because seed fall is usually accompanied by leaf fall that covers up seeds, the latter usually reduces the seed dispersal by some animals, this method cannot realistically measure the actual events. For these reasons, this study uses a natural method for monitoring seed losses in natural conditions.

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This study focuses on the seed rain, soil seed bank, seed loss, and regeneration of *Castanopsis fargesii* Franch. (Fagaceae), a dominant tree species in the evergreen broad-leaved forests in Dujiangyan, SW China. Subtropical evergreen broad-leaved forest is a major vegetation type in China mainly dominated by evergreen broad-leaved tree species of Fagaceae, Lauraceae, Theaceae, Magnoliaceae, among others. It is mainly distributed in the Yangtze River (Changjiang) commonly known as subtropical evergreen broad-leaved forest (Wu, 1980; Zhong, 1997). More importantly, studies on seed dispersal and seed bank dynamics, especially of the dominant species, may greatly improve our understanding of the behavior of the whole ecosystem.

Specifically, we ask: (1) What is the nature of seed rains and seed bank dynamics of *C. fargesii*? (2) Is there mast seeding for *C. fargesii*? (3) For how long do seeds of *C. fargesii* remain on the ground in different years? (4) Do more seeds of *C. fargesii* remain on the ground in mast years than in regular years? (5) What are the relative contributions of seed rain and seed loss to natural regeneration of *C. fargesii*?

## 2. Materials and methods

### 2.1. Study area and site preparation

Our study site is located in the Dujiangyan region, a transition zone between Qingzang (Qinghai-Tibet) Plateau and Chengdu Plain on the western border of Sichuan Basin, southwestern China. Its altitude is 700–1500 m, and the annual precipitation ranges from 1200 to 1800 mm. The vegetation is evergreen broad-leaved forest with high species diversity (Wu, 1980; Chen, 2000a,b; Zhuang and Gao, 2002). At 700 m, where the permanent plots for the study were laid down, the annual average temperature is 15.2 °C with an average July temperature of 24.7 °C, an average January temperature of 4.6 °C, and a mean annual precipitation of 1243 mm (Chen, 2000a).

The study was carried out in a 90 m × 110 m permanent plot at 700 m (N31°04', E103°43') established in August 2000 for long-term forest dynamics research. The whole plot, subdivided into 396 5 m × 5 m quadrates (Fig. 1), was fenced with wire netting in early 2001 to avoid human disturbances, although it did not influence seed predation by most small mammals.

### 2.2. Spatial distribution patterns of *C. fargesii*

After the site was established, we measured the diameter at breast height (DBH) and tree height (*H*) for all trees with DBH ≥ 1 cm. For smaller trees (DBH < 1 cm or height < 1.3 m), we measured tree height and the diameter at the ground level. The locations of trees in each 5 m × 5 m quadrate were also recorded.

As a model species, we chose *C. fargesii*, a dominant tree species in the evergreen broad-leaved forests at our site, to examine its seed loss dynamics and natural regeneration. There were totally 331 trees ha<sup>-1</sup> with a height (*H*) of 10 m or taller and about half of them (170) were *C. fargesii*. We recorded a

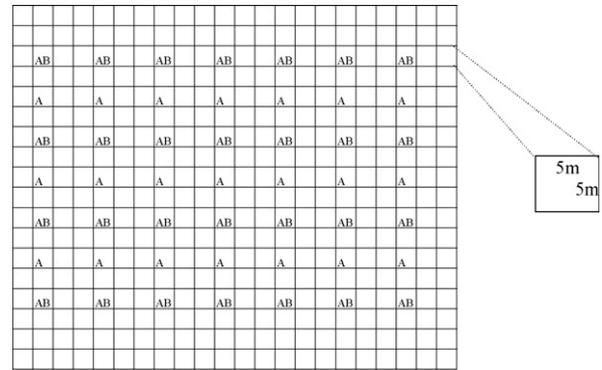


Fig. 1. Layout of the seed traps in evergreen broad-leaved forest at the study site in Dujiangyan, SW China. The seed traps of 1 m above the ground (aerial traps) and on the ground (ground traps) were represented by A and B, respectively; AB represents the aerial traps next to the ground traps in a 5 m × 5 m sample area.

total of 537 individual trees (*H* > 1.5 m) at this site with maximum DBH of 54.2 cm and the maximum *H* of 30.0 m. We identified three growing stages for *C. fargesii*: seedling (*H* ≤ 1.5 m), sapling (1.5 m < *H* ≤ 10 m), and adult plant (*H* > 10 m). New seedlings (1-year old) were identified by the typical cotyledons and non-woody stems (old seedlings >1-year having leaves and woody stems). In December 2002, all new seedlings in the plot were recorded in each 5 m × 5 m quadrate.

### 2.3. Seed rain, seed loss, and soil seed bank measurements

Seed fall and seed loss were measured using seed traps. The seed traps, with circular iron wire frame, were made of vinylon cloth (mesh size = 2 mm). The diameter of the mouth of the traps was 79.8 cm so that the actual sampling area of each trap was 0.5 m<sup>2</sup>. In late September 2001, we set up 49 aerial traps 1-m above the ground using bamboo posts to prevent predation by terrestrial vertebrates and 28 evenly spaced ground traps. Every ground trap was placed near a corresponding aerial trap within 0.5–1 m (Fig. 1). The total areas sampled by the 49 aerial traps and 28 ground traps were 24.5 and 14 m<sup>2</sup>, respectively. The collected materials in each trap was sorted into the following categories: sound seeds (with sound viable cotyledons), seeds infected by larvae (larval-infested seeds), seeds eaten by rodents, immature seeds, aborted seeds, cups, leaves, twigs, and other debris.

For the aerial traps, the number of seeds and the contents in each trap were recorded more frequently (e.g., every 2–5 days) when seeds were abundant and less frequently in the other parts of the year. After each measurement, all the contents in the aerial traps were scattered randomly on the ground below the aerial traps. For the ground traps, the number of seeds and other contents in each trap were recorded at approximately monthly intervals from October 2001 to October 2004. After each counting, all contents were scattered in the same ground trap, so that the natural conditions could be maintained at all times.

We also sampled the seed bank by collecting nine litter and soil samples (0.5 m × 0.5 m) randomly at this permanent site with 2–3 months intervals, and the sampling was completed in

one day in each interval. We counted all the seeds of all species including that of *C. fargesii* in leaf-litter and humus in the sample units, separated soil samples at the depths of 0–2 cm, 2–5 cm and >5 cm, and counted the seeds in each sample by sieving. The collected materials in each sample unit were then classified into the following categories: sound seeds, larval-infested seeds, mildewy seeds, budding seeds, and others.

#### 2.4. Data analysis

We used Student's *t*-test to compare the observed variance/mean ratio ( $s^2/m$ ) of the tree density in each life stage in  $5\text{ m} \times 5\text{ m}$  quadrates with the theoretical one (1 indicates Poisson distribution with variance = mean) and calculated the coefficient of aggregation (CD;  $CD = s^2/m$ ) to examine the spatial distribution of *C. fargesii* with different size classes.  $CD > 1$  indicated objects with the clustered or aggregated spatial distribution patterns (Yin et al., 2005). We estimated the number of seeds dispersed by animals by comparing the seed densities between the aerial traps and the ground traps. To quantitatively describe the seed rain, seed fall and seed loss, we assume that (1) the seed production (seed input; seeds  $\text{m}^{-2}$ ) in the ground traps equals the seed production (seed input; seeds  $\text{m}^{-2}$ ) in the aerial traps, and (2) seed dispersers (e.g. rodents) do not remove seeds in the aerial traps. We estimated the number of seeds dispersed by animals by comparing the seed densities between the aerial and ground traps. Accordingly, we have the following equations:

$$G_i^L = G_i^F + G_{i-1}^R - G_i^R \quad (1)$$

$$G_i^F = A_i^F \quad (2)$$

From Eqs. (1) and (2), we have:

$$G_i^L = A_i^F + G_{i-1}^R - G_i^R \quad (3)$$

$$R_i^{AF} = R_i^{GF} = \frac{G_i^R}{t_i - t_{i-1}} \quad (4)$$

where  $G_i^L$  is the mean density of seeds lost from ground traps at the  $i$ th observation,  $G_i^F$  the mean density of seeds fall in the ground traps at the  $i$ th observation,  $G^R$  the mean density of seeds reserved in ground traps,  $G_{i-1}^R$  the mean density of seeds reserved in ground traps at  $(i - 1)$ th observation,  $G_i^R$  the mean density of seeds reserved in ground traps at the  $i$ th observation,  $A_i^F$  the mean density of seeds fall in the aerial traps at the  $i$ th observation,  $t_i$  the date at  $i$ th observation and  $R_i^{AF}$  and  $R_i^{GF}$  are the rate values of seed fall in aerial and ground traps.

### 3. Results

#### 3.1. Spatial distribution patterns of *C. fargesii*

The population of *C. fargesii* showed a weak bimodal frequency distribution in both DBH and height ( $H$ ) with abundant seedlings and mid-sized trees, indicating a multi-layer vertical structure and a complex age structure (Fig. 2). Trees of all size categories showed clustered or aggregated spatial distribution

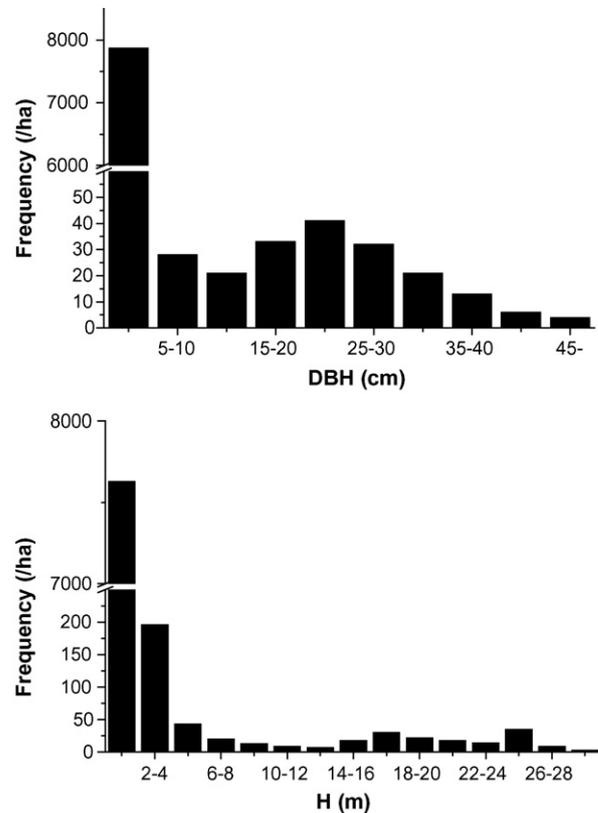
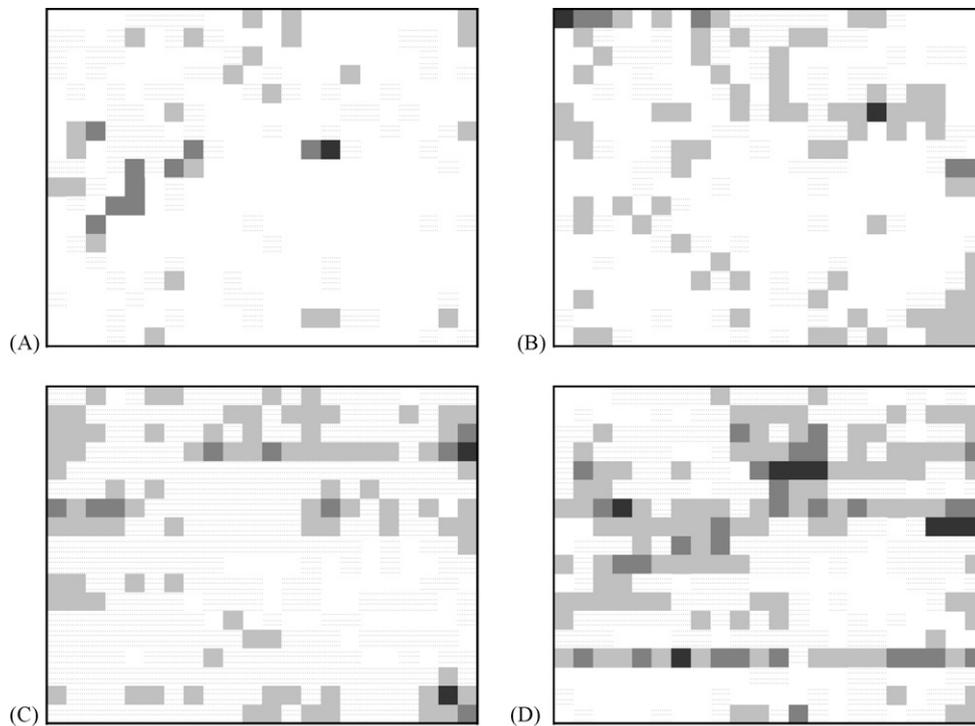


Fig. 2. Frequency distributions of breast-height diameter (DBH; top) and tree height ( $H$ ; bottom) of *C. fargesii* at the study site.

with strong associations between seedlings and adult trees (Fig. 3; Table 1). Student's *t*-test for variance/mean ratio ( $s^2/m$ ) showed that the ratios of adult plant ( $H > 10\text{ m}$ ), sapling ( $1.5\text{ m} < H \leq 10\text{ m}$ ), seedling ( $H \leq 1.5\text{ m}$ ), 1-year seedling and all trees of *C. fargesii* were all greater than 1, indicating aggregated spatial distributions in these groups (Table 1). However, *t*-tests on coefficient of aggregation (CD) showed that the CD values also indicated that levels of spatial aggregation were very different among the groups, i.e. seedlings of  $H \leq 1.5\text{ m}$  were mostly aggregated, followed by 1-year seedlings, saplings, and adult trees (Table 1).

#### 3.2. Seed rain

The annual seed production varied greatly from year-to-year (Fig. 4A). Total annual sound seed productions were 73.37, 5.12 and 19.56 seeds  $\text{m}^{-2}$  in 2001, 2002 and 2003, respectively. The fall of sound seeds of *C. fargesii* lasted about 3 months in 2001 (2 October–30 December 2001), 2 months in 2002 (28 October–27 December 2002), 3 months in 2003 (6 October 2003–4 January 2004), and there was a relatively long period of seed rain (including sound seeds, larval-infested seeds, seeds eaten by rodents, immature seeds, abort seeds, and cups). The maximum rate values of seed fall in aerial traps were 7.06 (on 28 October 2001), 0.18 (on 12 November 2002) and 0.63 (on 10 November 2003) seeds  $\text{m}^{-2}\text{ day}^{-1}$  (Table 2, Fig. 4A). The average weight of a single sound seed was 0.426 g so that the total sound seed productions were  $>312.56$ ,  $>21.81$ ,  $>83.33\text{ kg ha}^{-1}$  (consider-



Type No. of individual Symbol	A: H > 10 m	B: 1.5 m < H ≤ 10 m	C: H ≤ 1.5 m	D: 1-yr seedling
	0	0	0	0
	1	1	1-25	1-5
	2	2-5	26-75	6-15
	3	6-10	76-125	16-25
	4	≥ 11	≥ 126	≥ 26

Fig. 3. Spatial distribution of *C. fargesii* in the permanent study site. (A–D) Adult plant ( $H > 10$  m), sapling ( $1.5 \text{ m} < H \leq 10$  m), seedling ( $H \leq 1.5$  m), and 1-year seedling, respectively.

ing seed losses before seed fall from the tree crown) in 2001, 2002 and 2003, respectively. The mean annual sound seed productions were more than  $326,800 \text{ seeds ha}^{-1} \text{ year}^{-1}$ , i.e.  $139.22 \text{ kg ha}^{-1} \text{ year}^{-1}$  between 2 October 2001 and 1 October 2004.

### 3.3. Ground seed density and seed loss

Sound seeds were found in ground traps in 2001 (20 October 2001–21 April 2002), 2002 (26 November 2002–8 May 2003) and 2003 (10 October 2003–7 June 2004), respectively. The maximum mean seed densities on the ground

were 28.06 (23 November 2001), 2.14 (26 November 2002) and 9.47 (16 December 2003) seeds  $\text{m}^{-2}$  (Fig. 4B; Table 2). The peak seed densities on the ground were delayed for about 26, 14 and 36 days after the peak seed rain density in 2001, 2002 and 2003, respectively. The maximum rates of seed loss from the ground traps were 1.20 (23 November 2001), 0.05 (26 November 2002) and 0.28 (14 November 2003) seeds  $\text{m}^{-2} \text{ day}^{-1}$  (Fig. 4C; Table 2). The maximum rates of seed loss from the ground traps were delayed for about 26, 14 and 4 days after the peak seed rain density in 2001, 2002 and 2003, respectively.

Table 1

Results of student's *t*-test of variance/mean ratio for adult plant, sapling, seedling and 1-year seedling of *C. fargesii*

Statistics	A: Adult plant ( $H > 10$ m)	B: Sapling ( $1.5 \text{ m} < H \leq 10$ m)	C: Seedling ( $H \leq 1.5$ m)	D = A + B + C	E: 1-year seedling
Mean ( $\bar{m}$ )	0.42	0.93	19.03	19.91	5.63
Variance ( $s^2$ )	0.53	2.64	508.60	470.16	48.63
$s^2/\bar{m} = \text{CD}$	1.28	2.85	26.73	23.62	8.64
Observed <i>t</i>	3.89	25.98	361.53	317.82	107.37

$N = 396$ , d.f. = 395, and  $t_{0.001} = 3.32$  for all variables.  $N$  is the total number of quadrats;  $s^2/\bar{m}$  is the variance/mean ratio;  $t_{0.001}$  is one-sided critical value at 0.001 level. Analysis was based on 396 individual quadrats of  $5 \text{ m} \times 5 \text{ m}$ .

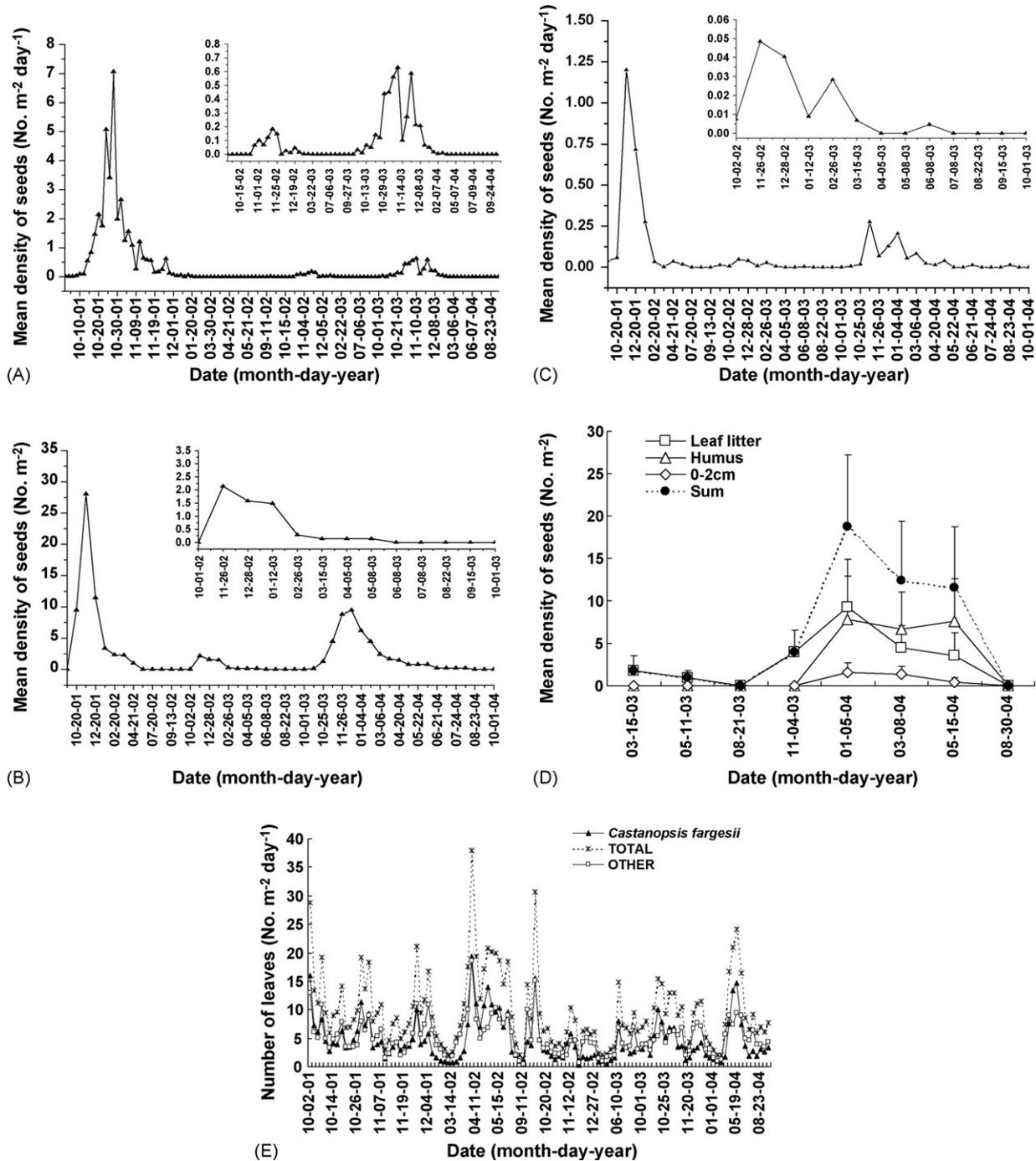


Fig. 4. Temporal changes in sound seed rain collected from the aerial traps (A), mean density of sound seeds observed from ground traps (B), the mean rate of sound seed lose on the ground (C), sound seed bank (D) of *C. fargesii*, and leaf fall of *C. fargesii* and other species (E) in evergreen broad-leaved forest in Dujiangyan, SW China, from 2 October 2001 to 1 October 2004. The insets in (A)–(C) show the changes during short periods of time. Error bars in (D) represent standard error of the mean (S.E.M.).

### 3.4. Soil seed bank dynamics

In general, seed density was high in the litter/humus layers and declined with soil depth. The number of seeds in litter/soil bank varied greatly over time. Seed bank dynamics corresponded well with seed rain dynamics in the same year (Fig. 4A and D). We found only one seed in the layer of 2–5 cm depth soil and no seeds in soil deeper than 5 cm. In August 2003 and 2004, we found no sound seeds in the seed banks.

## 4. Discussion

### 4.1. Spatial distribution patterns and population dynamics

All size categories of *C. fargesii* showed clustered or aggregated spatial distribution and the levels of spatial aggregation were very different among groups, i.e. the seedlings of  $H \leq 1.5$  m were mostly aggregated, followed by 1-year seedlings, saplings, and adult trees (Table 1; Fig. 3). The

Table 2

Comparisons of the maximum values of some items on sound seed of *C. fargesii* between 2 October 2001 and 1 October 2004

Items	The sound seed density in ground traps at a specific time (no. m <sup>-2</sup> )	Rate of sound seed fall in the ground traps (no. m <sup>-2</sup> day <sup>-1</sup> )	Rate of sound seed losses from ground traps (no. m <sup>-2</sup> day <sup>-1</sup> )	Accumulative sound seeds in the ground traps in 12 months (no. m <sup>-2</sup> )	The annual seed productions (no. m <sup>-2</sup> )
A	28.06	7.06	1.20	73.37	81.51
B	2.14	0.18	0.05	5.12	7.88
C	9.47	0.63	0.28	19.56	31.71
D	13.22	2.62	0.51	32.68	40.37
A/B	13.11	39.22	24.00	14.33	10.34
A/C	2.96	11.21	4.29	3.75	2.57
A/D	2.12	2.69	2.35	2.25	2.02
B/D	0.16	0.07	0.10	0.16	0.20
C/D	0.72	0.24	0.55	0.60	0.79

A is the (maximum) value observed between 2 October 2001 and 1 October 2002; B is the (maximum) value between 2 October 2002 and 1 October 2003; C is the (maximum) value between 2 October 2003 and 1 October 2004; D is the average value of A, B, and C. Rate of seed fall in ground traps = rate of seed fall in aerial traps. Accumulative seeds in ground traps = accumulative seeds in aerial traps. The annual seed productions were expediently estimated by the sum of sound seeds and larval-infested seeds in this study.

different levels of spatial aggregation measured by CD of trees of different age (or size) groups strongly indicate the role of competition. As seedlings or trees grow larger, competition leads to more even distribution of trees over space (Table 1). Also, pathogens could also play a role in producing these patterns. The highly aggregated seedlings suggest that either seeds are highly spatially aggregated or certain unevenly distributed microhabitats over space promote seed germination and/or seedling survival (Guo, 1998). However, the spatial aggregation of seeds might only occur after dispersal because adult trees that produce seeds are more evenly distributed over space. He et al. (1997) also reported that spatial patterns shift from high clumping to looser intensity or random distribution when moving from juveniles to adults for the same species in a Malaysian tropical rain forest. The frequency distribution in DBH and height indicate that *C. fargesii* population has a multi-layer vertical structure and complex age structure (Fig. 2). *C. fargesii* is clearly regenerating successfully in this ecosystem, as evidenced by massive seedlings observed at the site (Figs. 2 and 3). Abundant seedlings contribute to *C. fargesii* population recruitment, which helps maintain its dominance in the evergreen broad-leaved forest. Overall, *C. fargesii* has a relatively stable population in the evergreen broad-leaved forest in the region (Figs. 2 and 3).

#### 4.2. Seed production and seed rain

Although the difference between the number of cups and acorns can be used to estimate losses of acorns on the tree, cup fall may be the best estimate for acorn production (Shaw, 1968). However, it was difficult to estimate the rate of acorn loss in a canopy based on the difference between the number of cups and the number of seeds (Shaw, 1968; Sork et al., 1993; Xiao et al., 2001). In our study, we estimated the annual seed production of *C. fargesii* as the sum of both sound and larval-infested seeds collected from the aerial traps (see also Xiao et al., 2001). However, this might underestimate the total seed production because some seeds might be lost due to possible predation and dispersal before falling into the traps. The annual seed

productions were 81.51, 7.88 and 31.71 seeds m<sup>-2</sup> in 2001, 2002 and 2003, respectively (Table 2). Xiao et al. (2001) reported that seed production of *C. fargesii* in a primary forest of the same region in 2000 was about 1.9 seeds m<sup>-2</sup>. The sound seed production of *C. fargesii* in the mast year (2001) was 14.33 and 3.75 times of that in the regular years, 2002 and 2003, respectively (Table 2). Mast seeding (synchronous highly variable seed production among years; Shaw, 1968; Janzen, 1971; Sork et al., 1993; Kelly, 1994; Crawley and Long, 1995) is a widespread and extensively discussed, but still puzzling, phenomenon (Ree et al., 2002). Mast seeding is often treated as an adaptive reproductive trait overlaid on the direct influence of weather (Kelly and Sork, 2002). The time of the seed fall and its sustained period indicate the species' high adaptation to environmental changes (Ban, 1995). The reproduction and regeneration of *C. fargesii* with the mast and regular seed years might be a co-evolutionary product although we still lack a good understanding of the underlying mechanisms. Long-term study could help understand the role of inter-annual variation of seed production and the interspecific associations with other plants, mammals, and microbes. A related study by Peng et al. (2000) showed that the sound seed production of *C. fargesii* was 72.3 seeds m<sup>-2</sup> at Chongqing Simian Mountain (N28°30', E106°20') in 1996, which was quite close to the mast value in our observation. Liu and Zhong (2000) experimental study also showed that the mean value of seed production over 3 years was 50.5 seeds m<sup>-2</sup> on Fanjing Mountains (N27°49', E108°45'). Clearly, seed production of the same species was quite variable and long-term research is needed to better document the spatial and temporal variations.

#### 4.3. Natural seed loss, predator satiation and seedling recruitment

Our study shows that seed rain density, seed density on the ground, seed loss, and seed bank are highly dynamic and may affect the recruitment of *C. fargesii* in complex ways. Seed removal rates and seed fates differ with species, season, year, site, and even among replicates within sites. Moreover, this

study also showed strong interactions among these effects, as previously noticed in a Neotropical forest by Brewer and Rejmánek (1999). We observed not only 2,414 seeds of *C. fargesii* but also 12,283 seeds of other species such as *Cyclobalanopsis glauca* (Thunb.) Oerst., *Quercus glandulifera* Bl., *Cornus controversa* Hemsl., *Pittosporum tobira* (Thunb.) Ait., *Platycarya strobilacea* Sieb. et Zucc., *Kalopanax pictus* (Thunb.) Nakai, and *Symplocos laurina* (Retz.) Wall. (X.-J. Du, unpublished data). The seed banks of other species were quite large in the evergreen broad-leaved forests, which could mitigate the predation pressure and prolong the preservation of *C. fargesii* seeds. So, the local germination of *C. fargesii* may be enhanced.

The fallen leaves cover the fallen seeds thus reduce the dispersed probability from predation to some extent (see also Jarvis, 1964; Shaw, 1968; Myster and Pickett, 1993). The fall of leaves of most species and the seeds of *C. fargesii* occurred almost simultaneously (Fig. 4E), protecting seeds of *C. fargesii* from predation. Leaf size of *C. fargesii* is similar to or smaller than many other species such as *Cyclobalanopsis glauca* (Thunb.) Oerst., *Quercus glandulifera* Bl., *Cornus controversa* Hemsl., and *Symplocos laurina* (Retz.) Wall. (X.-J. Du, unpublished data). Yet, the rate of seed loss can vary greatly among microhabitats (e.g. Hay and Fuller, 1981; Whelan et al., 1991; Gill and Marks, 1991; Schupp, 1995; Guo, 1998; Sun and Chen, 2001). Seed density and seed loss of *C. fargesii* on the ground were highly dynamic (Fig. 4B and C). After 20 January 2002, the rate of seed loss from ground traps declined (Fig. 4C), possibly due to predator satiation in the mast year of 2001 (Fig. 4B). Predator satiation had been reported in many studies (e.g. Crawley and Long, 1995; Vander Wall, 1997; Curran and Leighton, 2000; Kelly et al., 2000; Schnurr et al., 2002) and was considered as the result of co-evolution between plants and seed-dispersers (Janzen, 1969, 1971; Smith, 1970; Li and Zhang, 2001). In this study, some seeds of *C. fargesii* were also preserved on the ground for a prolonged time in the regular years of 2002 and 2003 although the seed abundance was lower in 2002 and 2003 than in 2001. Predator satiation in both mast and regular years would result in non-interrupted increased seed germination. Our findings also showed that the localized regeneration opportunity of *C. fargesii* is increased through longer persistence period of seeds on the ground and the high production of sound seeds in mast years corresponds with predator satiation that plays a critical role in natural regeneration. The predator satiation of *C. fargesii* contributes to the dominance and stability of its population, which in turn might enhance the stability of the entire ecosystem.

The study area has many small mammal species, including *Niviventer confucianus* Milne-Edwards, *N. fulvescens* Gray, *Berymys bowersi* Anderson, *Leopoldams edwardsi* Thomas, and *Rattus nitidus* Hodgson that may serve as main seed dispersers for tree species (Xiao et al., 2002). Although there is no detailed information on the species-specific selection of seeds by these small mammals, there is no doubt that small mammals help forest regeneration by dispersing plant propagules. Insect infestation and predation by rodents are the key factors affecting seed fates in seed rain and seed banks

(Xiao, 2003). Seed dispersal by small mammals can promote forest regeneration in several ways: (1) seed dispersal can reduce density-dependent mortality of seeds or seedlings (“Escape Hypothesis”; Janzen, 1970; Connell, 1971; Howe and Smallwood, 1982); (2) seed dispersal could lead to more “safe sites” for species as described by the “colonization” hypothesis (Howe and Smallwood, 1982; Willson and Traveset, 2000); (3) “directional dispersal” to particularly favorable sites may also provide selective advantages to the plant (Howe and Smallwood, 1982; Venable and Brown, 1993).

The seed banks of *C. fargesii* varied greatly with time and soil depth (Fig. 4D). Seed bank dynamics is clearly related to the seed rain dynamics in the corresponding year. We found that seedling emergence in the upper soil (i.e. under the fallen leaves, 0–1 cm and 1–2 cm depth soil layer) is usually higher than in deeper soils (X.-J. Du, unpublished data), partly because seeds show similar distribution in the soil (Fig. 4D). It is surprising that we found no sound seeds of *C. fargesii* in the seed banks in August 2003 and 2004 (Fig. 4D), suggesting low over-year persistence of *C. fargesii* seeds in the seed bank and high seedling emergence from previous year’s seed rain. Seed rain, seed ground density, seed loss, and leaf fall were highly dynamic and certain quantity of seeds were preserved on the ground for a prolonged time due to predator satiation in both the mast and regular years so that the continuous presence of seed bank and seedling recruitments *in situ* became possible. Both longer time observations and manipulative experiments should be carried out to better understand the roles of seed dispersal and regeneration process in the ecosystem performance.

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## References

- Ban, Y., 1995. Evolution of life history strategy in plants. *Chin. J. Ecol.* 14, 33–39.
- Brewer, S.W., Rejmánek, M., 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *J. Veg. Sci.* 10, 165–174.
- Chen, C.D., 2000a. Biodiversity Research and Conservation of Dujiangyan, China. Sichuan Science and Technology Press, Chengdu, China.
- Chen, C.D., 2000b. The Dujiangyan region—Pivot sector of assemblage, differentiation and maintenance of biodiversity in northern part of Hengduan Mountain. *Acta Ecol. Sinica* 20, 28–34.
- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J., Gradwell, G.R. (Eds.), *Dynamics of Populations*. PUDOC, Wageningen, The Netherlands, pp. 298–310.
- Crawley, M.J., Long, C.R., 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *J. Ecol.* 83, 683–696.

- Curran, L.M., Leighton, M., 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70, 101–128.
- Dalling, J.W., Muller-Landau, H.C., Wright, S.J., Hubbell, S.P., 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *J. Ecol.* 90, 714–727.
- Fenner, M., 2000. *Seed: The Ecology of Regeneration in Plant Communities*, 2nd ed. CABI Publishing, Wallingford, UK.
- Fuentes, M., 2002. Seed dispersal and tree species diversity. *Trends Ecol. Evol.* 17, 550.
- Gill, D.S., Marks, P.L., 1991. Tree and shrub seedling colonization of old-fields in central New York. *Ecol. Monogr.* 61, 183–205.
- Guariguata, M.R., Pinard, M.A., 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. *For. Ecol. Manage.* 112, 87–99.
- Guo, Q., 1998. Microhabitat differentiation in Chihuahuan Desert plant communities. *Plant Ecol.* 13, 71–80.
- Hay, M.E., Fuller, P.J., 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology* 62, 1395–1399.
- He, F.L., Legendre, P., LaFrankie, J.V., 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. *J. Veg. Sci.* 8, 105–114.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201–228.
- Hughes, L., Westoby, M., 1990. Removal rates of seeds adapted for dispersal by ants. *Ecology* 71, 138–148.
- Janzen, D.H., 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23, 1–27.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528.
- Janzen, D.H., 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2, 465–492.
- Jarvis, P.G., 1964. Interference by *Deschampsia flexuosa* (L.) Trin. *Oikos* 15, 56–78.
- Kalin, Arroyo, M.T., Cavieres, L.A., Castor, C., Humaña, A.M., 1999. Persistent soil seed bank and standing vegetation at a high alpine site in the central Chilean Andes. *Oecologia* 119, 126–132.
- Kelly, D., 1994. The evolutionary ecology of mast seeding. *Trends Ecol. Evol.* 9, 465–470.
- Kelly, D., Harrison, A.L., Lee, W.G., Payton, I.J., Wilson, P.R., Schaubert, E.M., 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos* 90, 477–488.
- Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: why, how, where? *Ann. Rev. Ecol. Syst.* 33, 427–447.
- Li, H.J., Zhang, Z.B., 2001. Relationship between animals and plant regeneration by seed. II. Seed predation, dispersal and burial by animals and relationship between animals and seedling establishment. *Biodiv. Sci.* 9, 25–37.
- Liu, J.M., Zhong, Z.C., 2000. Nature of seed rain, the seed bank and regeneration of a *Castanopsis fargesii* community on Fanjing Mountain. *Acta Phytocol. Sinica* 24, 402–407.
- Myster, R.W., Pickett, S.T.A., 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos* 66, 381–388.
- Peng, J., Li, X.G., Fu, Y.C., Liu, Y.C., 2000. Seed rain and seed bank of constructive species in evergreen broadleaved forest at Chongqing Simian Mountain. *Chin. J. Appl. Ecol.* 11, 22–24.
- Ree, M., Kelly, D., Bjørnstad, O.N., 2002. Snow tussocks, chaos, and the evolution of mast seeding. *Am. Nat.* 160, 44–59.
- Schnurr, J.L., Ostfeld, R.S., Canham, C.D., 2002. Direct and indirect effects of masting on rodent populations and tree survival. *Oikos* 96, 402–410.
- Schupp, E.W., 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82, 399–409.
- Shaw, M.W., 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. I. A preliminary study of acorn production, viability and losses. *J. Ecol.* 56, 565–583.
- Smith, C.C., 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.* 40, 349–371.
- Sork, V.L., Bramble, J., Sexton, O., 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74, 528–541.
- Sun, S.C., Chen, L.Z., 2001. The effects of animal removal and groundcover on the fate of seeds of *Quercus liaotungensis*. *Acta Ecol. Sinica* 21, 80–85.
- Vander Wall, S.B., 1997. Dispersal of singleleaf pinon pine (*Pinus monophylla*) by seed-caching rodents. *J. Mammal.* 78, 181–191.
- Venable, D.L., Brown, J.S., 1993. The population-dynamic functions of seed dispersal. *Vegetatio* 107/108, 31–55.
- Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends Ecol. Evol.* 17, 379–385.
- Wang, W., Ma, K.P., 1999. Predation and dispersal of *Quercus liaotungensis* acorns by Chinese rock squirrel and Eurasian jay. *Acta Bot. Sinica* 41, 1142–1144.
- Wang, W., Ma, K.P., 2001. Predation and dispersal of *Quercus liaotungensis* Koidz. acorns by animals in Dongling Mountain, Northern China. I. Effect of rodents removal on loss of acorns. *Acta Ecol. Sinica* 21, 204–210.
- Wang, W., Ma, K.P., Liu, C.R., 1999. Removal and predation of *Quercus liaotungensis* acorns by animals. *Ecol. Res.* 14, 225–232.
- Wenny, D.G., 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. *Ecol. Monogr.* 70, 331–351.
- Whelan, C.J., Willson, M.F., Tuma, C.A., Souza-Pinto, I., 1991. Spatial and temporal patterns of postdispersal seed predation. *Can. J. Bot.* 69, 428–436.
- Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd ed. CABI Publishing, Wallingford, UK, pp. 85–110.
- Wu, Z.Y., 1980. *Vegetation in China*. Science Press, Beijing, China.
- Xiao, Z.S., 2003. Effects of small mammals on tree seed fates and forest regeneration in Dujiangyan region, China. Ph.D. Dissertation. Institute of Zoology of the Chinese Academy of Sciences.
- Xiao, Z.S., Wang, Y.S., Zhang, Z.B., 2001. Seed bank and the factors influencing it for three Fagaceae species in Dujiangyan region Sichuan. *Biodiv. Sci.* 9, 373–381.
- Xiao, Z.S., Wang, Y.S., Zhang, Z.B., Ma, Y., 2002. Preliminary studies on the relationships between communities of small mammals and habitat types in Dujiangyan region Sichuan. *Biodiv. Sci.* 10, 163–169.
- Yin, Z., Guo, Q., Ren, H., Peng, S.L., 2005. Seasonal changes in spatial distributions of two desert annual plants. *Plant Ecol.* 178, 189–199.
- Zhong, Z.C., 1997. Present situation and prospect of ecological studies on evergreen broad-leaved forest in China. In: Zhong, Z.C. (Ed.), *Advance in Plant Ecology*. Southwest Normal University Press, Chongqing, China, pp. 44–45.
- Zhuang, P., Gao, X.M., 2002. The concept of the rainy zone of West China and its significance to the biodiversity conservation in China. *Biodiv. Sci.* 10, 339–344.