

# Community Dynamics of Seed Rain in Mixed Evergreen Broad-leaved and Deciduous Forests in a Subtropical Mountain of Central China

Ze-Hao Shen<sup>1\*</sup>, Yuan-Yuan Tang<sup>1</sup>, Nan Lü<sup>1</sup>, Jun Zhao<sup>1</sup>, Dao-Xing Li<sup>2</sup> and Gong-Fang Wang<sup>2</sup>

(<sup>1</sup>Department of Ecology, College of Environmental Sciences, the Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China;

<sup>2</sup>National Dalaoling Forest Park, Yichang 435000, China)

## Abstract

Seed dispersal is a key process within community dynamics. The spatial and temporal variations of seed dispersal and the interspecific differences are crucial for understanding species coexistence and community dynamics. This might also hold for the mixed evergreen broadleaved and deciduous forests in the mountains of subtropical China, but until now little existing knowledge is available for this question. In 2001, we chose to monitor the seed rain process of our mixed evergreen broad-leaved and deciduous forest communities in Mount Dalaoling National Forest Park, Yichang, Hubei Province, China. The preliminary analyses show obvious variations in seed rain density, species compositions and timing of seed rain among four communities. The average seed rain densities of the four communities are  $2.43 \pm 5.15$ ,  $54.13 \pm 182.75$ ,  $10.05 \pm 19.30$  and  $24.91 \pm 58.86$  inds./m<sup>2</sup>, respectively; about one tenth the values in other studies in subtropical forests of China. In each community, the seed production is dominated by a limited number of species, and the contributions from the others are generally minor. Fecundity of evergreen broadleaved tree species is weaker than deciduous species. The seed rain of four communities begins earlier than September, and stops before December, peaking from early September to late October. The beginning date, ending date and peak times of seed rain are extensively varied among the species, indicating different types of dispersal strategies. According to the existing data, the timing of seed rain is not determined by the climate conditions in the same period, while the density of seed rain may be affected by the disturbances of weather variations at a finer temporal resolution.

**Key words:** interspecific difference; Mount Dalaoling; mountain mixed evergreen broad-leaved and deciduous forests; seed rain; species composition; weather effect.

Shen ZH, Tang YY, Lü N, Zhao J, Li DX, Wang GF (2007). Community dynamics of seed rain in mixed evergreen broad-leaved and deciduous forests in a subtropical mountain of central China. *J. Integr. Plant Biol.* 49(9), 1294–1303.

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Seed dispersal has been emphasized in ecology for different reasons. It is a basic approach of population migration for plant species to respond environmental change, and an important dimension of niche differentiation among species. So, seed dispersal has long been viewed as a crucial mechanism for

species coexistence and community dynamics (Beyer 1975; Howe and Smallwood 1982; Nanthan and Muller-Landau 2000; Ronce 2001; Fenner and Thompson 2005). Within the life history of a population, the “seed fecundity–dispersal–germination” stage is most sensitive to environmental variations, and holds the key for the responses of plant species to environmental selection, and adaptive evaluation (Tilman 1997; Wang and Smith 2002; Clark et al. 2004), and has attracted more and more emphases in plant ecology and biogeography in the past twenty years (Fenner 1985; Schupp and Fuentes 1995; Levin et al. 2003).

Seed rain is the first stage and the main part of seed dispersal. Temporal (either inter- or intra- the process) and spatial variations in quantity and species composition are the basic characteristics of community seed rain, resulting in differences in community types, age of parent trees, climatic variation, natural

Received 23 Feb. 2006 Accepted 9 Jul. 2006

Supported by the National Natural Science Foundation of China (30000024, 30470313).

\*Author for correspondence.

Tel: +86 (0)10 6275 1179;

Fax: +86 (0)10 6275 1179;

E-mail: <shzh@urban.pku.edu.cn>.

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doi: 10.1111/j.1672-9072.2007.00530.x

**Table 1.** Seed rain density by species in four types of forest communities

Species name	Density (mean $\pm$ SD) (seeds/m <sup>2</sup> )			
	I	II	III	IV
<i>Quercus glandulifera</i> var. <i>brevipetiolata</i>	1.03 $\pm$ 3.27		0.15 $\pm$ 0.49	0.14 $\pm$ 0.74
<i>Castanea henryi</i>	0.48 $\pm$ 2.39	1.09 $\pm$ 0.33		
<i>Corylus chinensis</i>	0.75 $\pm$ 2.74	1.14 $\pm$ 0.27		
<i>Clethra fargesii</i>	0.18 $\pm$ 1.11		0.45 $\pm$ 1.19	0.55 $\pm$ 1.21
<i>Meliosma oldhamii</i>		171.98 $\pm$ 31.40		
<i>Tapiscia sinensis</i>		73.18 $\pm$ 21.17		
<i>Sycopsis sinensis</i>		1.67 $\pm$ 0.37		
<i>Castanea seguinii</i>		1.10 $\pm$ 0.20	0.2 $\pm$ 0.52	
<i>Magnolia springeri</i>		0.75 $\pm$ 0.17		
<i>Cyclobalanopsis glauca</i>		0.57 $\pm$ 0.13		
<i>Dendrobenthamia japonica</i> var. <i>chinensis</i>		0.55 $\pm$ 0.10	0.25 $\pm$ 0.79	0.10 $\pm$ 0.56
<i>Sorbus folgneri</i>			7.8 $\pm$ 18.87	1.79 $\pm$ 5.16
<i>Fagus lucida</i>			0.05 $\pm$ 0.22	5.24 $\pm$ 8.75
<i>Cornus hemsleyi</i>			0.3 $\pm$ 0.98	0.38 $\pm$ 1.32
<i>Acer oliverianum</i>			0.75 $\pm$ 2.67	
<i>Cornus controversa</i>				0.31 $\pm$ 1.23
<i>Cyclocarya paliurus</i>				0.25 $\pm$ 1.12
<i>Acanthopanax evodiaefolius</i>				16.03 $\pm$ 57.57
<i>Cyclobalanopsis myrsinaefolia</i>			0.1 $\pm$ 0.45	
<i>Lyonia ovalifolia</i> var. <i>lanceolata</i>				0.07 $\pm$ 0.37
<i>Daphniphyllum macropodum</i>				0.034 $\pm$ 0.19
Total	2.43 $\pm$ 5.15	54.13 $\pm$ 182.75	10.05 $\pm$ 19.30	24.91 $\pm$ 58.86

SD, standard deviation. I, *Carpinus hupeana*–*Corylus chinensis* forest; II, *Corylus chinensis* forest; III, *F. lucida*–*Q. glandulifera* var. *brevipetiolata* forest; IV, *Fagus lucida* forest.

disturbance, habitat heterogeneity, spatial autocorrelation, etc. (Walker and Neris 1993; Loiselle et al. 1996; Tang et al. 1998; Wang et al. 2000; Hardesty and Parker 2002; Han and Wang 2002; Shen et al. 2004). With a hierarchical Bayesian simulating model, Clark et al. (2004) assessed an 11-year data of seed rain of forest communities in the southern Appalachian. Instead of supporting the trade-off of seed fecundity and dispersal strategies in the community, their data indicated significant contributions to biodiversity from environmental heterogeneity and stochasticity, as well as species and individual specific responses, indicating that the variation of community seed rain and the interaction with environmental factors deserve more exploration.

In the mountains of subtropical China, the mixed evergreen broad-leaved and deciduous forests (MEDFs) possess very complicated spatial-temporal structure and species composition, and host a lot of deciduous rare tree species endemic to China (Wu 1985; Shen et al. 1999). The coexistence of these species with distinctive phylogenetic origins and ecological properties has long been an intriguing question and is still open to exploration. The understanding of seed fecundity and the dispersal process is of particular interest. However, published reports are sparse (Liu 1999; Shen et al. 2004). In this study,

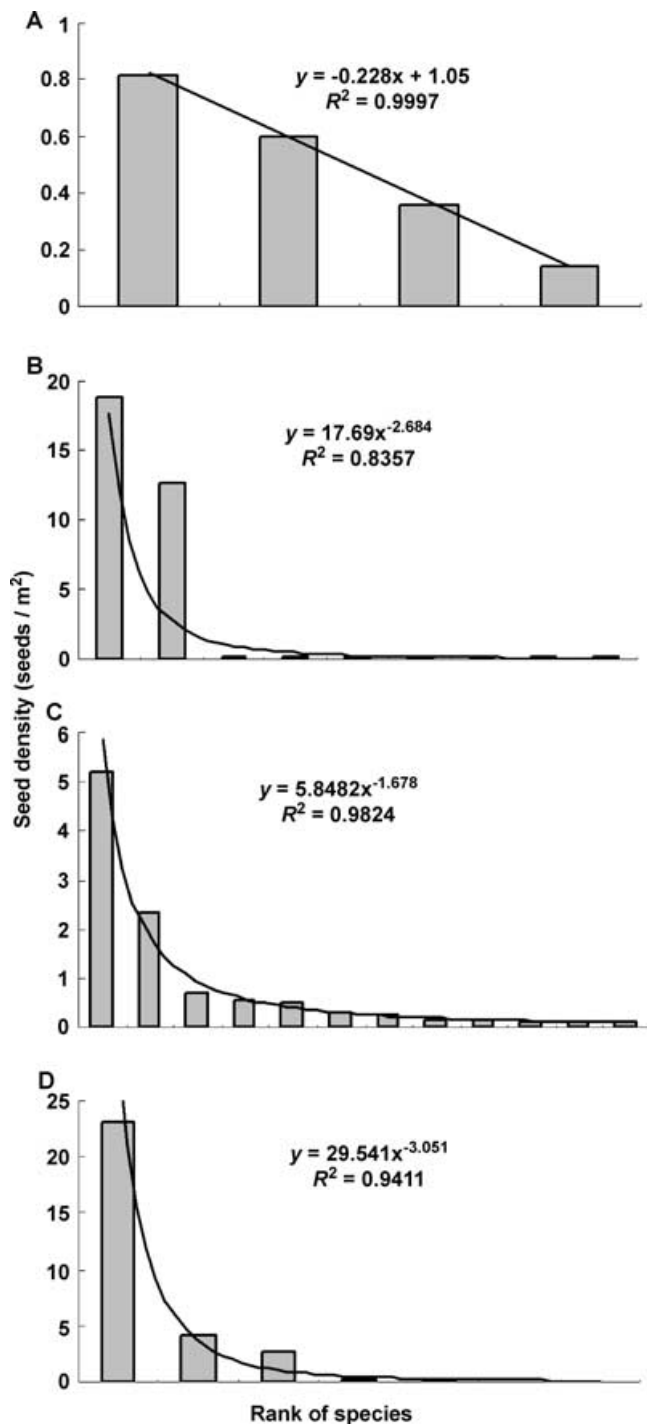
preliminary investigations into the characteristics of seed rain of MEDFs were based on our work at Mt. Dalaoling in the Three Gorges of the Yangtze River. Our specific objectives were to determine: (1) the basic quantitative characteristics of seed rain, and the variations among different communities; (2) the temporal aspects of seed rain and variation among community types; and (3) the variation of seed rain among species.

## Results

According to the species compositions on four sites, we named the communities as site I – *Carpinus hupeana* & *Corylus chinensis* forest; site II – *C. chinensis* forest, site III – *Fagus lucida* and *Quercus glandulifera* var. *brevipetiolata* Forest; and site IV – *Fagus lucida* forest.

### Density of community seed rain

The average density of seed rain of four communities in 2001 is 18.81 ind./m<sup>2</sup>. Among them, the seed rain densities for community types I, II, III, IV are 1.92 seeds/m<sup>2</sup>, 32.48 seeds/m<sup>2</sup>, 10.44 seeds/m<sup>2</sup>, and 30.40 seeds/m<sup>2</sup>, respectively (Table 1).



**Figure 1.** The decreasing ranks of species seed rain densities of four communities.

The grey bars indicate the species-specific records of average seed rain density in the specific community. The black lines are the fitted models of frequency distribution of seed rain density in the communities. **A, B, C, D** corresponds to the community I, II, III and IV in the text, respectively.

### Species composition of seed rain

For each of the four communities, we ranked the tree species according to the average seed rain density (Figure 1). The gradient of density change followed power function in the *Corylus chinensis* forest (II), the *F. lucida*–*Quercus glandulifera* var. *brevipetiolata* forest (III), and the *Fagus lucida* forest (IV). A linear trend was observed in the *Carpinus hupeana*–*Corylus chinensis* forest (I), mainly because the seed rains of all species were very weak. It was similar for the four communities that only a few species dominate the quantity of community seed rain. Numbers of canopy species of four communities were 29, 27, 36 and 34, respectively, while only seven, 12, nine and four species were recorded in the seed rain in 2001, indicating that the majority of parent trees had no seed production at all.

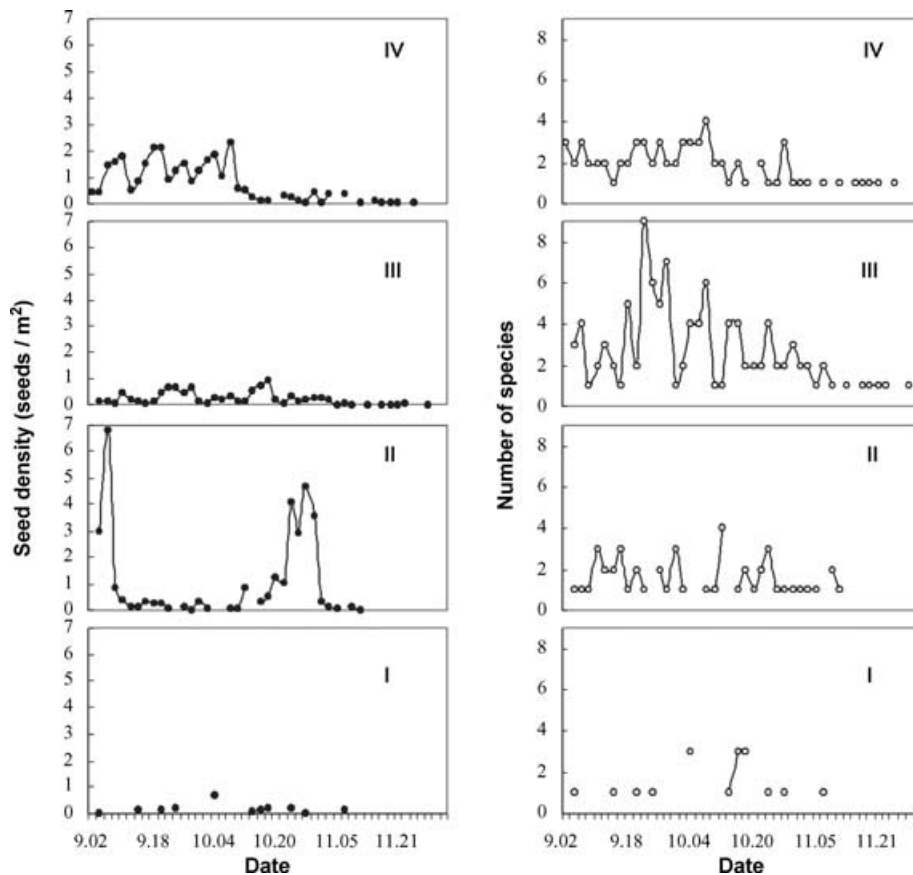
In *Corylus chinensis* forest (II), the dominant species of canopy only had a minor seed yield, while two companion species *Meliosma oldhamii* and *Tapiscia sinensis* contributed 97.1% of community seed rain. In the *F. lucida*–*Quercus glandulifera* var. *brevipetiolata* forest (III), the top three species contributed 78.8% of community seed rain, and 32.55% of canopy importance value, though the dominant species *Quercus glandulifera* var. *brevipetiolata* only contributed little to community seed rain. In the *Fagus lucida* forest (VI), *Acanthopanax evodiaefolius*, *F. lucida*, and *Sorbus folgnieri* contributed 83.3% of community seed rain. These three species also accounted for 78.5% of the value in canopy. All species in the *Carpinus hupeana*–*Corylus chinensis* forest (I) had minor seed fecundity, resulting in a very low value of community seed rain density.

A total of 64 tree species appeared in the sampling plots of four sites, 17 of which were evergreen broadleaved species, corresponding to 10.98% of importance value. Within 21 tree species of seed rain, only four were evergreen, with a 0.56% contribution to community seed rain.

### Temporal change of community seed rain

The temporal changes of density and species number of seed rain in four communities revealed that the process of seed rain in 2001 started earlier than 2 September (Figure 2). Although the measurement missed the starting part, we could still find that:

1. According to the sequence of density and species number of seed rain, the order of ending dates of this process in four communities are as following: *Carpinus hupeana* – *Corylus chinensis* forest (7 November), *Corylus chinensis* forest (11 November), *Fagus lucida* forest (25 November), *F. lucida* – *Quercus glandulifera* var. *brevipetiolata* forest (29 November). The altitudinal ranges of four communities were 1380–1420 m, 1300–1320 m, 1450–1490 m, and 1420–1460 m respectively. The stop dates for two communities on the south slope with higher elevations



**Figure 2.** The temporal change of density and species number of seed rain of four communities.

I, II, III, IV indicate the community types as in Table 1.

were later than the two on the north slope with lower elevations.

- Seed rain mainly occurred from early September to the end of October, with obvious spatial variation. Two peaks appeared in seed rain density of the *Corylus chinensis* forest, but the temporal change of species number also followed the one peak pattern, just as it happened in the other three communities. After a high value period, seed rain lasted for another period in low values before finally stopping.
- There were irregular periodic waves in seed rain density and species number during seed rain periods. It was more obvious in the *Fagus lucida* and *F. lucida* – *Quercus glandulifera* var. *brevipetiolata* forests, with a quasi-period of 3–5 days, while the other two forests showed quite different patterns.

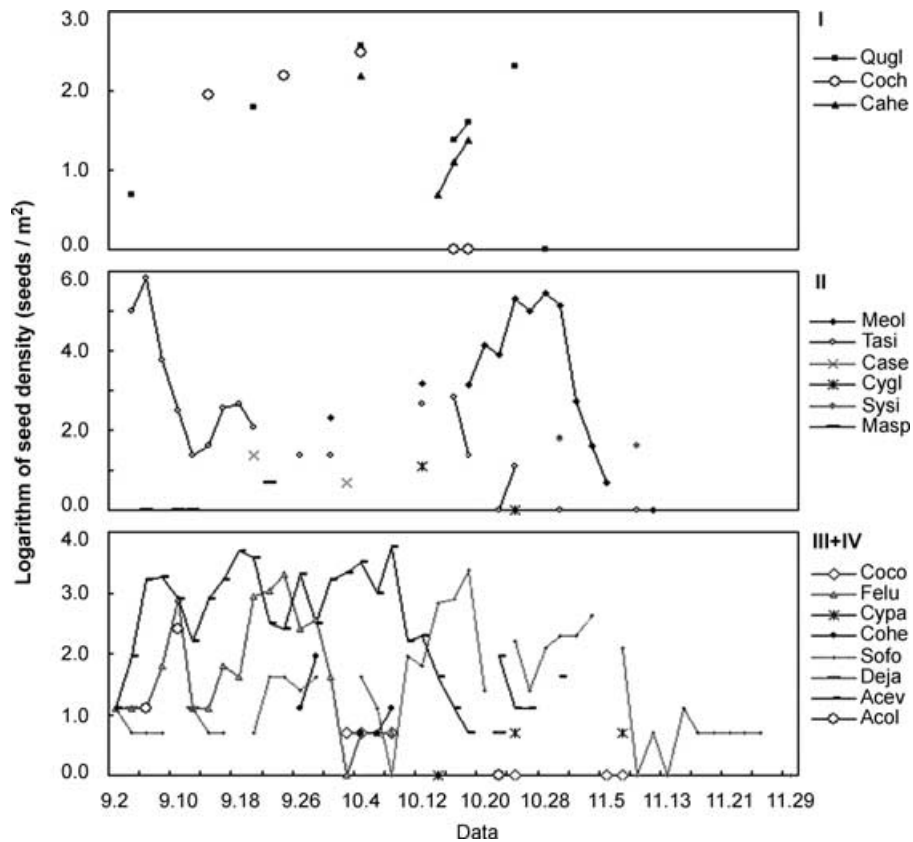
#### Temporal variation of seed rain for different species

Because the sampling sites of the *Fagus lucida* forest and the *F. lucida* – *Quercus glandulifera* var. *brevipetiolata* forest were

relatively near each other, we merged the data for species analysis. The records of seed rain processes for different species are shown in Figure 3. Those species with less than three records were excluded.

The seed rain processes of *Corylus chinensis*, *Quercus glandulifera* var. *brevipetiolata*, *Meliosma oldhamii*, *Tapiscia sinensis*, *Fagus lucida*, *Sorbus folgeri*, and *Acanthopanax evodiaefolius* in 2001 were comparatively complete in the 2001 records (Figure 3), while only partial information for some other species was revealed. Although the seed rain had begun for the communities in early September, the starting and ending dates, extension, and the peak values were drastically different among species.

According to the records from the same community, differences of seed rain can be found among species. In community I, *Quercus glandulifera* var. *brevipetiolata* had a longer seed rain than *Corylus sinensis* (55 d vs 35 d), by starting earlier and stopping later. But the peak times of both are more or less overlapped, from the end of September to early October. In community II, the seed rain period of *Tapiscia sinensis* (67 d) and *Meliosma oldhamii* (43 d) were partially overlapped, with the



**Figure 3.** The records of seed rain process of different species in three types of community.

I, *Carpinus hupeana*-*Corylus chinensis* community, II, *Corylus sinensis* community; III + IV, *Fagus lucida*-*Quercus glandulifera* var. *brevipetiolata* community. Acev, *Acanthopanax evodiaefolius*; Acol, *Acer oliverianum*; Cahe, *Castanea henryi*; Case, *Castanea seguinii*; Coco, *Cornus controversa*; Coch, *Corylus chinensis*; Cygl, *Cyclobalanopsis glauca*; Cypa, *Cyclocarya paliurus*; Deja, *Dendrobenthamia japonica* var. *chinensis*; Falu, *Fagus lucida*; Masp, *Magnolia sprengeri*; Meol, *Meliosma oldhamii*; Qugl, *Quercus glandulifera* var. *brevipetiolata*; Sofo, *Sorbus folgeri*; Sysi, *Sycopsis sinensis*; Tasi, *Tapiscia sinensis*.

peak times departing obviously, the former at 2–8 September, the later at 20 October to 1 November. In communities III and IV, *Sorbus folgeri* showed the longest seed rain period (89 d), with the peak time occurring from the middle of October until early November. The peak times of seed rain of *Acanthopanax evodiaefolius* (59 d) and *Fagus lucida* (37 d) both departed from that time; the former from early to late September, the latter from early September to mid-October. Compared with *Sorbus folgeri*, *Fagus lucida* had a shorter and more intensive seed rain process.

For other species, only relatively sparse seed rain was recorded in 2001, not enabling us to reveal the complete “start-peak-end” pattern of the whole process. According to the starting date of seed rain records, these species are ranked as follows: *Dendrobenthamia japonica* var. *chinensis* (4 September to 22 October), *Magnolia sprengeri* (6–22 September), *Castanea seguinii* (20 September to 2 October), *Cornus hemsleyi* (26 September to 8 October), *Castanea henryi* (26 September

to 10 October), *Cornus controversa* (2 October to 7 November), *Cyclobalanopsis glauca* (12–24 October), *Sycopsis sinensis* (30 October to 9 November).

## Discussion

### Seed rain between different community types

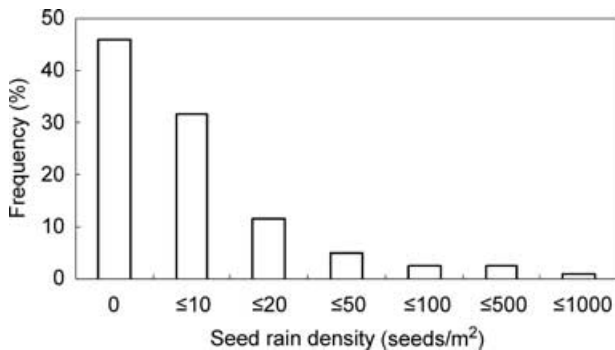
There are huge differences of seed rain density among different vegetation types (Molau and Larsson 1999). Within the same community type, the seed rain is also drastically heterogeneous (Schupp and Fuentes 1995; Loiselle et al. 1996). Compared with records of several subtropical forest communities in China (Table 2), our data on seed rain density is lower by one order of magnitude, while the numbers of species are comparable.

In contrast to the typical way of sampling the seed rain of a community, we tried to observe the spatial variation of seed

**Table 2.** Comparison of the arboreal seed rain of tree species of several types of communities

Community type	Latitude	No. species	Seed rain density (seeds/m <sup>2</sup> )	Reference
Mixed E-D forests at Dalaoling	31°01'–31°08' N	4–11	2.4–54.1	–
<i>Fagus lucida</i> mixed forest	27°49'–28°01' N	14	236.5	Liu 1999
Karst mixed E-D forest	25°09'–25°20' N	18	565.2	Liu 2000
<i>Castalopsis fargesii</i> forest	27°49' N	11	448.6	Liu and Zhong 2000

E-D, evergreen and deciduous.

**Figure 4.** Frequency distribution of seed rain density of all sampling records.

rain at two scales of seed rains of different community types by choosing a relatively mature and homogeneous section. We also documented the topographic variation within a community, for example, ridges, valley bottoms, shady slopes and sunny slopes. Overall, the average densities of seed rain had differences of one order of magnitude among the communities, and two orders of magnitude among all 120 traps (Figure 4), with up to 55 traps having zero records. Only 3.33% of traps captured enough seeds that were comparable to those in other studies. However, since all of these results came from one year of data, why was seed rain so low there?

First of all, Figure 2 shows that our sampling began a bit late, missing the beginning of the seed rain. According to our sampling on one of the communities in following years, the seed rain begins in mid-August, although it is normally sparse during the early stages. So the complete seed rain density should be slightly higher.

Loiselle et al. (1996) mentioned that their seed rain records were different on three occasions among five communities, and suggested that there could be significant differences between traps in the gaps and understories. Our work has also encountered significant differences in seed rain density (and species composition) related with topographical positions (Shen et al. 2004). Studies on the structure and dynamics of communities in mountain forests have suggested that the communities at upper slopes tend to be older, more stable and larger in biomass, while communities at the lower slopes and valley bottoms are more frequently disturbed by surface processes (i.e. landslides), and are younger, smaller in biomass, and in an earlier stage of

succession (Nagamatsu et al. 2003). So, it is reasonable to infer that the seed production of a heterogeneous, dynamic forest landscape is also heterogeneous in space, with the average value much lower than certain stands in it.

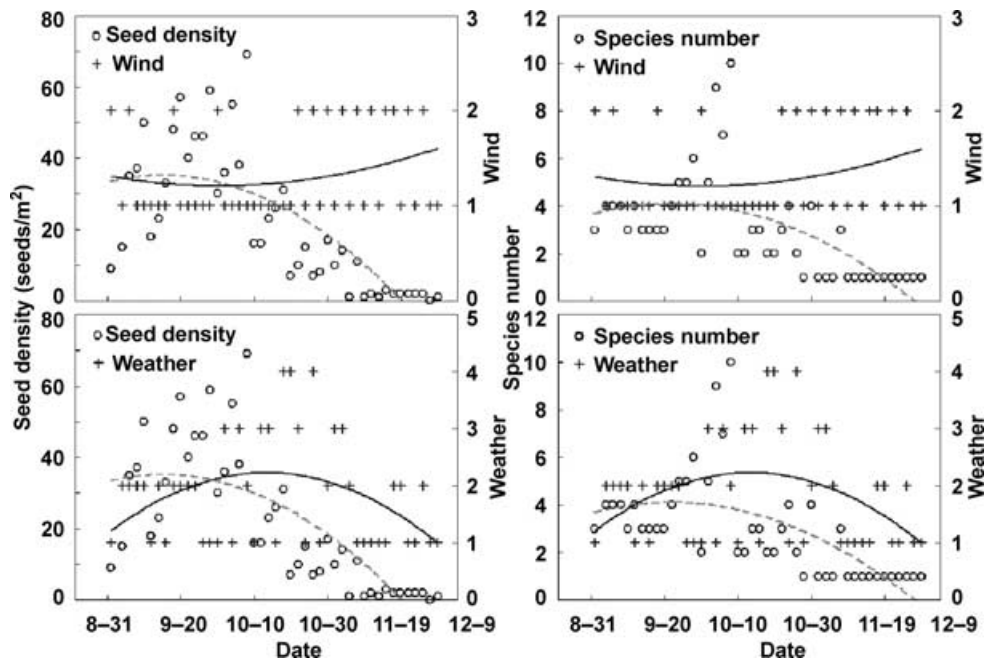
The temporal differentiation of mastering among species within a community, as a result of adaptive co-evolution in reproductive strategies is widely recognized (Fenner and Thompson 2005). In our monitoring of one of the communities – the mastering year of *Carpinus fargesii* – which was the dominant species at site II had only been recorded once in 4 years (but not this year) (Shen ZH., unpubl. data, 2004). The seed rain contribution from *Corylus chinensis* – the dominant species at site I – was also negligible in the recorded year, although we seemed to meet the mastering year of two other companion species. Does this mean that the results from one year's data are not valid for estimating the average seed rain of the communities?

Interannual variations in seed rain are mainly affected by temporal variation of climate (Howe and Smallwood 1982), while the spatial variation of local climate is mainly caused by topographic variation (Strahler and Strahler 1987). Species in a community have individualistic responses to environmental variations (Gleason 1926). This is also supported by the differentiation of mastering rhythms for the species within a community. So, given the drastic interannual variation in seed fecundity for a specific species, and also for a relatively homogeneous community dominated by just one or a few species, it is reasonable that, the annual seed productivity is much more stable in a heterogeneous forests landscape that is composed of a variety of species-rich and structure-complex community patches.

Although all of these factors have to be taken into consideration, further work is required to validate the different data obtained from different sources, and explore more information on the spatial and temporal variation of seed fecundity and dispersal.

#### Difference between evergreen and deciduous species

Generally, in the secondary succession process of mixed evergreen broadleaved and deciduous forests in the Chinese subtropical region, the importance of evergreen species tends to increase (Hao and Wei 1999; He and Chen 1995), but this hypothesis has never been validated by a regeneration processes. According to our data, the species number of evergreen trees



**Figure 5.** The seed rain process of *Fagus lucida*–*Quercus glandulifolia* var. *brevipetiolata* community and concurrent weather change in 2001.

The dash lines indicate the trend of seed rain quantity (for **A**, **C**) or species number in seed rain (for **B**, **D**); the solid lines indicate the trends of wind in **A**, **B** (1 – no wind; 2 – windy), and weather type in **C**, **D** (1 – fine; 2 – somber; 3 – shower; 4 – median rain).

in four communities comprised 26.56% of the total number of tree species, and contributed 10.98% of the importance value in the canopy. However, in seed rain, the ratio of species numbers of evergreen trees is 19.05%, and contributes only 0.56% to the total seed rain density, indicating the sexual reproductive capacity of evergreen species on average is lower than that of deciduous species, and the capability of seed reproduction cannot be the driving force for the evergreen species to lift their status in community succession.

### Climate influence at different scales

The temporal variation of seed dispersal processes has been related to concurrent climatic variation (Walker and Neris 1993; Nathan et al. 2000). There were short-term waves in our seed rain measurement (Figure 2). Was this relevant to the climatic dynamics? For technical reasons, we only recorded simple weather conditions on the sampling dates. Wind (two classes: 1, no wind; 2, windy) and rainfall (four classes: 1, fine; 2, somber; 3, small rain; 4, middle rain) were considered. Figure 5 shows the concurrent changes of seed rain density in the *Fagus lucida* and *Quercus glandulifera* var. *brevipetiolata* community and weather conditions. At a coarser resolution, there were less weather perturbations during the peak seed rain period in this community, while the density and species number of seed rain decreased quickly in the

following period with higher frequency of rain and wind. No significant correlation was found between seed rain and weather conditions of the same date ( $R_{\text{wind}-\text{No. seed}} = -0.229$ ,  $P = 0.135$ ;  $R_{\text{wind}-\text{No. species}} = -0.231$ ,  $P = 0.132$ ;  $R_{\text{rain}-\text{No. seed}} = 0.241$ ,  $P = 0.115$ ;  $R_{\text{rain}-\text{No. species}} = 0.185$ ;  $R_{\text{rain}-\text{No. seed}} = 0.228$ ). It seems that, the duration of the seed rain process is not directly determined by the weather during the seed rain period, but may be determined by the energy accumulation, as well as the degree of seed maturity attained by development in the whole growing season.

However, the heterogeneity of the climate also exists at finer temporal scales, such as the occurrence of flurries or showers, acting as a kind of short-term disturbance if they are intense enough. According to field observations, the daily variation of seed rain intensity might have a closer relationship with short-term weather perturbations. But also, more precise measurements are needed to validate this hypothesis in long-term monitoring.

## Materials and Methods

### Site conditions

The study area is located in the National Dalaoling Forest Park at approximately 110°52'–111°01' E, 31°01'–31°08' N, which lies

**Table 3.** The importance values of the first 10 species in four communities

Community types		I	II	III	IV
Characteristics of sampling plots	Elevation (m)	1300–1310	1360–1400	1420–1460	1450–1495
	Aspect	North	North	South	South
	No. seed traps ( $\times 1 \text{ m}^2$ )	30	40	20	30
Species name					
<i>Carpinus hupeana</i> Hu.		17.16	7.08		
<i>Corylus chinensis</i> Franch.		10.24	30.38		
<i>Clethra fargesii</i> Franch.		7.5	2.59	7.19	
<i>Castanea henryi</i> Rehd. et Wils.		7.16			1.62
<i>Fagus engleriana</i> Seem.		6.79			
<i>Betula luminifera</i> H. Winkl.		5.85	2.75		
<i>Lithocarpus cleistocarpus</i> (Seem.) Rehd. & Wils.		5.72			
<i>Cornus controversa</i> Hensl.		5.43			
<i>Quercus glandulifera</i> var. <i>brevipetiolata</i> (DC.) Nakai		4.24		10.87	1.21
<i>Juglans cathayensis</i> Dode.		1.87			
<i>Acer wilsonii</i> Rehd.			9.93		
<i>Meliosma oldhamii</i> Maxim.			8.04		
<i>Sycopsis sinensis</i> Oliv.			4.16		
<i>Tapiscia sinensis</i> Oliv.			3.84		
<i>Populus</i> sp.			3.71		
<i>Machilus ichangensis</i> Rehd. & Wils.			2.56		
<i>Fagus lucida</i> Rehd. et Wils.				13.62	63.87
<i>Cyclobalanopsis myrsinaefolia</i> (Bl.) Oerst.				8.06	
<i>Castanea seguinii</i> Dode.				7.93	
<i>Pieris formosa</i> (Wall.) D. Don				7.45	5.5
<i>Sorbus folgneri</i> (Schneid.) Rehd.				6.67	5.39
<i>Dendrobenthamia japonica</i> var. <i>chinensis</i> (Osborn) Fang				5.54	1.85
<i>Litsea ichangensis</i> Gamble				4.41	
<i>Cyclocarya paliurus</i> (Batal.) Iljinskaja				4.34	
<i>Acanthopanax evodiaefolius</i> Franch.					9.25
<i>Lyonia ovalifolia</i> var. <i>lanceolata</i> (Wall.) D. Don					4.57
<i>Rhododendron augustinii</i> Hemsl.					1.56
<i>Cerasus clarifolia</i> Yü et Li					1.07

I, *Carpinus hupeana*–*Corylus chinensis* forest; II, *Corylus chinensis* forest; III, *F. lucida*–*Q. glandulifera* var. *brevipetiolata* forest; IV, *Fagus lucida* forest.

near the dam of the Three Gorges Reservoir. This region is characterized by deeply incised mountain landforms, and a rich, antique and endemic flora (Chen et al. 1994; Shen et al. 1999). The geological substrate of Mt. Dalaoling is mostly composed of granite of the middle and late Azoic Era. The climate in this region is of a northern subtropical type, with a warm, humid summer, while showing an obvious altitudinal change. The average annual temperature is 8.5°C, average temperatures in January and July are –2.7°C, 19.2°C respectively (data obtained from a nearby weather station [1670 m a.s.l.]). The annual average precipitation is 1446.8 mm. Although the majority of precipitation occurs in summer, there is still 179.6 mm in winter occurring as snow and sleet (Zhang et al. 1990).

In accordance with the general conditions in the Three Gorges region, evergreen broadleaved forests in Dalaoling are only seen below 1300 m a.s.l.; deciduous forests basically distribute

above 1700 m. The MEDFs exist in a belt between 800–1700 m (Chen et al. 1994; Shen et al. 2000), normally dominated by deciduous *Fagus lucida* Rehd. et Wils., *Fagus engleriana* Seem., *Castanea henryi* Rehd. et Wils., *Quercus glandulifera* var. *brevipetiolata* (DC.) Nakai, *Castanea seguinii* Dode., and several species of *Carpinus* while evergreen *Cyclobalanopsis myrsinaefolia* (Bl.) Oerst., *Cyclobalanopsis multinervis* Cheng et T. Hong, *Quercus engleriana* Seem., *Lithocarpus cleistocarpus* (Seem.) Rehd. et Wils., *Litsea elongate* (Wall. ex Nees) Benth., *Litsea coreana* var. *lanuginosa* Levl., *Sycopsis sinensis* Oliv. are also common.

#### Survey of canopy composition

Within the altitudinal range of MEDFs in the Dalaoling National Forest Park, four sites were selected for vegetation sampling



and seed rain monitoring on account of community variation (Table 1). Considering the topographic variation of the community structure, sampling plots for community survey  $20 \times 20$  m in area were set at different topographic positions on each site. All individuals with a diameter at breast height (DBH) of  $\geq 2.5$  cm were recorded by species name, DBH, height and number. Data on each site were merged to show the difference of species composition of communities (Table 3).

### Seed rain measurement

The seed-traps were designed to have an area of  $1 \text{ m}^2$  and a depth of 0.6 m, with a round framework of iron line. The trap bags were made of a plastic net with a 1 mm pore diameter. When set up, the frameworks of seed-traps were kept horizontal, 1.0 m above the ground. All of the seed-traps were coded.

Seed-traps were set in four communities. Five repeating seed-traps were set randomly at each site of different topographic positions. In total, 30, 40, 20, and 30 seed-traps were assigned to sites I, II, III and IV, respectively and the seed rain sampling areas are  $30 \text{ m}^2$ ,  $40 \text{ m}^2$ ,  $20 \text{ m}^2$ , and  $30 \text{ m}^2$ , respectively (Table 1).

We collected the seeds in all seed traps once every 2 days from 2 September until the end of the seed rain in 2001. We went on collecting seed rain once every 10 days from January to June in 2002. The survey was stopped in July, as we found that the monthly variation of the community seed rain followed a curve of a single peak value. Then we focused our monitoring of seed rain only on sites III and IV after 2002, where the communities were dominated by *Fagus lucida* Rehd. et Wils.

Species of seeds were identified according to the trees from which the seeds fell. Seed samples were stored in paper packages, labeled with the codes of the seed-traps and the date of collection. The numbers of seeds were recorded in order of seed-trap, topographic positions, and date of collection.

### Data analysis

The following two formulas were used to count seed rain density and species richness of four communities and the composing species:

Seed rain density:  $D (\text{seeds/m}^2) = \text{number of seeds (seeds)} / \text{seed trap area (m}^2)$

Species richness of seed rain:  $R (/m^2) = \text{Species number} / \text{seed trap area (m}^2)$

The species distributions of abundance of seed rain were fitted for each community with proper models (Figure 1).

We then plotted the temporal change of density and species richness of the seed rain processes recorded in four communities, and the species-specific temporal variations of seed rain were also plotted to compare the strategies of seed dispersal among species.

In analysis of the effects of rain and wind on seed rain, a spearman correlation index was calculated, and a *P*-value was estimated with SPSS10.0

## Acknowledgements

We are grateful to Zuo Wen-Chang for help in field work, and the Dalaoling National Forest Park for the long-term support of our study.

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(Handling editor: Jian-Ping Ge)