

# 濒危树种闽楠种子和幼苗生态学研究

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**摘要:**从 1995 至 1998 年, 通过种子收集器布设、不同程度圈围的样方处理, 实验室和野外发芽实验、相邻格子样方调查和土壤中种子的筛选等一系列方法, 对福建罗卜岩闽楠种质资源保护区内闽楠为优势的常绿阔叶林群落中闽楠种群的果实、种子库、种子散布、果实/种子捕食、种子萌发和幼苗存活等进行了研究。结果表明: 1995 至 1996 年果实量为 116 个/ $m^2$ , 成熟高峰期在 1996 年 1 月中旬, 1997 至 1998 年为 103 个/ $m^2$ , 成熟高峰期在 1997 年 12 月中旬, 1997 至 1998 年, 绝大部分 (90.1%) 的果实直接从母树上掉落, 低于 9.5% 的果实由鸟类传播。实验室的种子发芽率为 93%, 而在野外仅为 12%。野外发芽率低多由种子霉烂引起。闽楠的种子寿命较短, 其种子在次年 4 月初开始萌发, 7 月之后地面种子即丧失活力。动物捕食不仅影响种子的存活, 同时也影响幼苗的死亡率, 未经圈围与圈围的样地中被取食的果实和幼苗数量有显著差异。在新近形成的林窗中或远离母树均降低了果实的迁移和幼苗的死亡率, 但各因素交互作用有所不同。密度相关效应发生在 2~3 个月的幼苗阶段, 之后, 密度高低对果实被取食和幼苗死亡没有显著的影响。这些结果表明, 闽楠种子和幼苗经历较大的环境压力, 即在高湿度生境中母树树冠下的种子不仅易受到土壤病原菌的感染, 同样容易遭受动物所捕食, 从而导致较低的野外种子发芽率和幼苗存活率, 这是闽楠致濒的重要原因之一。

**关键词:** 闽楠; 果落; 种子库; 种子散布; 果实/种子捕食; 种子萌发; 幼苗存活

## Seed and seedling ecology of the endangered *Phoebe bournei* (Lauraceae)

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**Abstract:** To clarify regenerative traits and explore effects of canopy cover, density, distance, dispersers, or predators on fates of seeds or seedlings of *Phoebe bournei*, fruit fall, seed bank, seed dispersal, fruit/seed predation, seed germination and seedling survival were examined in a mid-subtropical evergreen broadleaf forest in Luoboyan Nature Reserve, southeastern China. Fruit production averaged 116 fruits/ $m^2$  between 1995 and 1996, and 103 fruits/ $m^2$  between 1997 and 1998. The peak of fruit ripening appeared in mid-January, 1996, and in mid-December, 1997. Most fruits (90.1%) fell directly from parent trees and less than 9.5 per cent were disseminated by birds between 1997 and 1998. Field and laboratory germination rate differed sharply with 93.0 per cent in laboratory compared to 12 per cent in the field. Poor field germination rate was mainly due to rotted seeds attacked by soil pathogens. *Phoebe* did not have a persistent seed bank strategy. Its seeds germinated in early April and were inviable after July. Predators affected

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**Brief introduction author:** WU Da-Rong (1966~), male, born in Fujian Province, PhD, associate professor. Research field: population ecology of rare and endangered plants.

not only seed survival, but seedling mortality as well. The number of predated fruits or lost seedlings in the unprotected plots differed significantly from that in the protected plots. Recent gaps or far distance from parent trees reduced fruit removal and seedling mortality, but their interaction was not always the case. Density dependence occurred in the very young seedling stage (about 2~3 months), but did not significantly affect fruit predation or mortality of seedlings more than 3 months. These results indicate that *Phoebe* seeds or seedlings suffer high environmental pressures, i.e., most seeds near parent trees in high moist habitats are susceptible not only to soil pathogens, but to high predation beneath parent trees' canopy as well, which results in poor field seed germination and seedling survival.

**Key words:** *Phoebe bournei*; fruit fall; seed bank; seed dispersal; fruit/seed predation; seed germination; seedling survival

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## 1 Introduction

In the life history of trees, the most drastic change in cohort population occurs in seed and seedling stages<sup>[1]</sup>, and many researchers have tried to elucidate detailed demography of these stages<sup>[2,3]</sup>. Seed rain, seed bank, seed shadow, seedling bank and seedling survival<sup>[4~6]</sup> are important life history processes that may be influenced by animal dispersers and seed or seedling predators as well as by spatiotemporal variation in the abiotic environment<sup>[7~9]</sup>. Seed banks are classified as (i) transient, when seeds can germinate soon after they are shed from the mother plant, and (ii) persistent, when seeds can remain in the soil in a state of dormancy<sup>[10]</sup>. A seed bank strategy is common for climax (or shade-tolerant) species<sup>[11]</sup>. But in tropical wet forests, later successional shade-tolerant tree species with large seeds do not have a long-lived seed bank<sup>[12]</sup>. The peaking time of fruit ripening plays an important role in seed dissemination by birds<sup>[13,14]</sup>. Among the variety of dispersal systems, bird dispersal is characterized by a wide distribution of seeds<sup>[15]</sup> and a high proportion of seeds removed from the vicinity of parent plants<sup>[16]</sup>. Canopy cover and resulting light conditions have been considered important for seed and seedling survival<sup>[17,18]</sup>. Seed survival increases in gaps where higher light level and lower humidity are inimical to plant pathogens<sup>[19]</sup>, and more danger and fewer resources to frugivores<sup>[18]</sup>. For seedlings, increased survival in gaps is attributed to not only lower predation, but faster growth rates as well<sup>[9]</sup>. Density-dependence has long been a paradigm for understanding the regulation of plant populations<sup>[20]</sup>. Many studies describe intraspecific competition by the use of the phrase "neighborhood effect"<sup>[21,22]</sup>. The main advantages to a plant of seed dispersal are colonization of "safe sites"<sup>[23]</sup> and escape from high mortality near parent plants<sup>[24]</sup>. Effects of distance from the conspecific adults on demographic variation of seeds and seedlings have been discussed by many researchers<sup>[3,25,26]</sup>. Previous studies have verified experimentally that higher seed/seedling density and/or greater proximity to the parent plant often, but not always, lower seedling recruitment<sup>[25]</sup>. Conversely, inverse density dependence, whereby higher density enhances survival, can arise due to predator satiation<sup>[27]</sup>. "Regenerative strategy"<sup>[28]</sup> is a useful concept to characterize the demographic traits of rare and endangered species<sup>[19,30]</sup>. Regeneration difficulty may cause populations of rare and endangered species to decrease<sup>[29]</sup>.

Little is known about regenerative traits of the endangered species, *Phoebe bournei* (Hemsl.) Yang<sup>[1]</sup>. In this study, we discussed regenerative traits of this species based on two years observation of fruit production, seed bank, seed dispersal, seed germination, fruit/seed predation and seedling survivorship. We addressed the following two questions: (1) does the regenerative traits explain the endangered situation of this species? (2) How do the environmental factors, viz. canopy cover, density, protection condition, or



distance affect fates of seeds or seedlings of this species?

## 2 Study site and species

The study was conducted in a secondary broadleaf forest in Luoboyan Nature Reserve (LNR) (26°26'30"N, 117°34'30"E, 642m a. s. l.), about 40 kilometers northeast of Sanming city, central area of Fujian Province in China. Regional climate is mid-subtropical with mean annual temperature 19.5°C and average annual precipitation 1643.2mm which usually falls between spring and summer. The frost free period lasts 297 days. *Phoebe bournei* (Hemsl.) Yang is an evergreen tree species endemic to southeastern China, and usually distributed in such moist environments as coves and sides of brooks. The largest *Phoebe* individual in LNR (1998) reaches 78.0cm *dbh* with the height more than 20.0m. Most individuals with *dbh*  $\geq$  20.0cm bear fruits. There are 112 mature trees per hectare. These parent trees produce elliptical oily fruits with 6.0~7.0mm in diameter, 1.0~1.5cm in length, composed of a thin exocarp, a fleshy mesocarp and a hard endocarp. Ripe fruits are dark and usually fall with no thalline exciple attaching them. So a newly fallen fruit is easily identified by the bright white color of its umbo. Some ripe fruits dehisce completely and from them seeds fall down directly. The seed body remains attached to the seedling during the first season of growth. One seed can produce, sometimes, as much as four seedlings due to polyembryony. Seedling emergence peaks in May. As a climax tree species, its seeds or seedlings can germinate or establish both beneath forest canopy and in light gaps<sup>[31]</sup>. In LNR, *Ph. bournei* is dominant in forest communities, or codominates with *Betula luminifera* Winkl., *Ilex formosana* Maxim., *Comptotheca acuminata* Decne, *Castanopsis tibetana* Hance, *Machilus pauhoi* Kanehira, and *Phoebe checkiangensis* C. B. Shang, covering more than 34hm<sup>2</sup><sup>[32]</sup>. Such large *Phoebe* dominant communities are seldom in other areas of its distribution region.

## 3 Methods

### 3.1 Observation of fruit production, dissemination, seed bank and seed germination

To quantify fruit production, 36 parent trees between 1995 and 1996, and 20 between 1997 and 1998, were selected in *Phoebe* dominant communities. Here, we defined "parent trees" as those individuals with *dbh*  $\geq$  20.0cm. Between 1995 and 1996, we positioned five 0.5m<sup>2</sup> wire framed fruit traps lined with polyethylene bags midway between the trunk and canopy edge of parent trees. Each trap was supported by four vertical polyvinyl chloride plastic pipes that were adjusted so that the receiving face was 1m above the ground. Traps were emptied every two days until the end of fruit fall. Between 1997 and 1998, we designed five 0.5m<sup>2</sup> closed plots and five 0.5m<sup>2</sup> open plots beneath each parent tree's canopy. The mesh size of the closed plots was designed into two types, 2×2mm<sup>2</sup> for four of them, and 4×4cm<sup>2</sup> for the other. The four plots allowed very few insects to enter from nearby ground, however, could not prevent insects from falling in from the top. At no time could fruits be removed outside these four plots. The other allowed insects, generally no rodents to enter, and fruits in this plot may very well be removed outside. All fruits in open plots could be removed or predated by insects, rodents or birds. In order to prevent fruits from bouncing into these plots, wire meshes were set up at the upper slope. Fruits were counted and marked with permanent colors every two weeks. Fruits in plots with 2×2mm<sup>2</sup> meshes were classified into three categories<sup>[13]</sup>: "directly fallen fruits", "bird-disseminated fruits" and "fruits attacked before dispersal". In this study, "bird-disseminated fruits" included seeds from dehiscing mature fruits, because fruits with exocarps and mesocarps removed could be not only seeds defecated by birds, but those seeds from dehiscing mature fruits as well. All traps or plots were placed from September to March next year. *Dbh* of each parent tree was measured. Thus, the fruit input per unit area in traps or differently treated plots was then calculated, based on 180 traps between 1995 and 1996, 80 plots with 2×2mm<sup>2</sup> meshes, 20 plots with 4×

4mm<sup>2</sup> meshes and 100 open plots between 1997 and 1998. The data between 1996 and 1997 were, however, not included, because fruit production of fail-year appeared to be significantly low.

The seed bank was measured during late June and September in 1998 (after germination, but before the onset of new seeds). 100 soil cores (each with a diameter of 40cm and depth of 9cm) were collected along transects. Soil samples were taken to a laboratory. The soil was then washed through a sieve, and seeds were separated from the retained organic material and small stones. To test viability, apparently sound seeds were sown in moist vermiculite in plastic bags at 21 C<sup>constant</sup>. Seeds were considered germinated when their radicles extended 5mm. In the field, apparently well developed fruits were directly sown in 10 closed plots. We counted seedlings from March to late June.

### 3.2 Examination of fruit/seed and seedling predation

Predation of fruit was examined at three sites, i. e., Qikeng, Shaosuo and Sigongli, from late October in 1997 to March next year. Unprotected plots of 50 × 50cm<sup>2</sup> were positioned beside protected plots of the same size. The mesh size of protected plots was 2 × 2mm<sup>2</sup>, allowing very few insects to enter. Each protected plot had a lid on. At each site, the experimental design was a completely randomized factorial with two levels of protection, two levels of density, and four replicates of each treatment. 800 fruits were sowed in these plots, with 400 fruits in protected plots and others in unprotected plots. Both in protected plots and in unprotected plots, 320 fruits were used for the treatment of "high density" (320 fruits/m<sup>2</sup>) and 80 fruits for "low density" (80 fruits/m<sup>2</sup>). We arbitrarily defined here 320 fruits/m<sup>2</sup> as "high density" and 80 fruits/m<sup>2</sup> as "low density" only because fruit fall was 116 fruits/m<sup>2</sup> between 1995 and 1996. 2400 fruits in all were used to monitor fruit predation affected by protection or density at three sites. Each selected fruit was well developed, undamaged, marked and randomly sowed on the surface of soil, contained in 50 × 50 × 70cm<sup>3</sup> wooden boxes, which were buried about 5cm below the soil surface. We counted fruits and replaced newly fallen fruits for rotten or lost ones in boxes every two weeks. From April, we planted 80 seedlings in each of four protected plots or four unprotected plots for "high density" treatment and 20 seedlings in each of the other protected plots or the other unprotected plots for "low density" treatment. It was the same way with the unprotected plots. We counted seedlings every two weeks from April to September, and classified dead seedlings into four categories<sup>[4]</sup>: (1) damping off, (2) herbivory, (3) physical damage and (4) unknown.

In order to examine effect of distance from parent trees, forest canopy, or interaction between them on predation of fruits, the experimental design was a completely randomized factorial with two levels of shading, i. e., beneath forest canopy vs. in forest gaps, two levels of distance, i. e., close to parent trees vs. far from parent trees, and four replicates of each treatment at each site. 16 50 × 50 × 70cm<sup>3</sup> boxes with 50 marked fruits (200 fruits/m<sup>2</sup>) in each box were buried 5cm below the soil surface. 2400 fruits in all were used in this experiment at three sites. Fruits remaining in boxes were counted every two weeks from late October in 1997 to March next year. We also replaced newly fallen fruits for rotted or lost ones in plots. All gaps were created from 1992 to 1996 with their sizes ranging from 150m<sup>2</sup> to 400m<sup>2</sup>, so could be treated as recent gaps. We arbitrarily defined, in this experiment, the distance of 100m away from the edge of a nearest mature tree's canopy as "long distance", and 10m as "short distance". From April in 1998, we planted 50 seedlings in each box and counted seedlings every two weeks from April to September. All dead seedlings were also classified into the above four categories.

### 3.3 Field test of neighborhood interference among seedlings

From late June to early July in 1998, 64 5 × 5m<sup>2</sup> contiguous grid quadrats were investigated to test neighborhood interference among seedlings of about 3 months old. All seedlings were counted and marked



on a piece of grid coordinate paper. When the distance between two stems was less than 10cm, we used vernier caliper to measure it. We arbitrarily defined 5cm as disturbing distance, because, based on the data of 1000 seedlings of about 3 months old, the length of each leaf averaged 3.5cm, and thus within 7cm, leaves from two neighboring seedlings overlapped (seedlings seldom furcated during the study). Dead seedlings were also counted, marked, and then classified into the above four categories.

#### 4 Results

##### 4.1 Fruit production, dissemination, seed bank and seed germination

Between 1995 and 1996, fruit fall began in early September and ended in late February next year, peaking in mid-January (Fig. 1). Between 1997 and 1998, fruits fell from October to early March next year, peaking in mid-December (Fig. 2). Fruit fall between 1995 and 1996 was 116 fruits/m<sup>2</sup>, ranging from 9 to 456 fruits/m<sup>2</sup>, while fruit fall in closed plots with 2 × 2m<sup>2</sup> meshes between 1997 and 1998 was 103 fruits/m<sup>2</sup>, ranging from 3 to 332 fruits/m<sup>2</sup> (Table 1). Of the 36 sampled trees between 1995 and 1996, 4 trees with *dbh* < 21.0cm did not produce fruits. Between 1997 and 1998, total fruit production amounted to 1.135 × 10<sup>6</sup> fruits/hm<sup>2</sup> (Table 2). Most fruits (90.1%) in plots with 2 × 2m<sup>2</sup> meshes had fallen directly from parent trees; 9.5 per cent of fruits (including seeds from dehiscing mature fruits) had been disseminated by birds, and only 0.4 per cent of fruits were destroyed by predispersal attack from insects. In this study, we found few seeds pierced by insects. Directly fallen fruits occurred one month earlier than bird-disseminated fruits (Fig. 3). Both of them peaked in mid-December, showing no time lag between them.

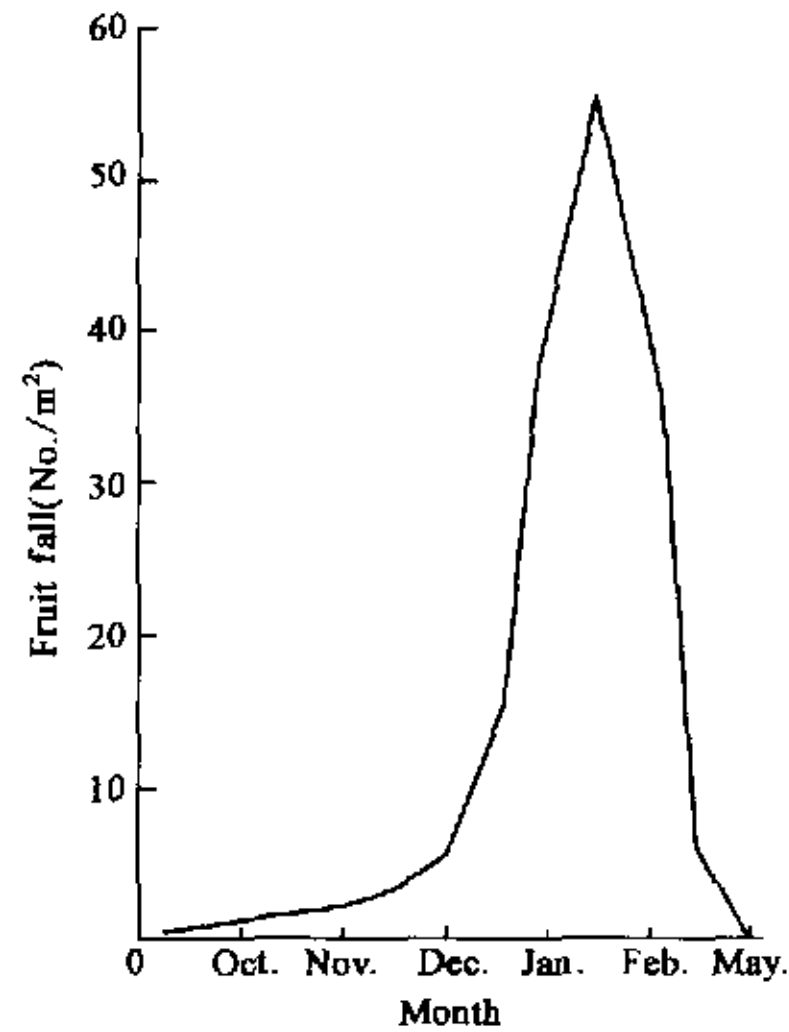


Fig. 1 Fruit fall in traps of 0.5m<sup>2</sup> between 1995 and 1996

Table 1 Fruit fall based on data from 32 parent trees between 1995 and 1996, and 20 parent trees between 1997 and 1998

Year	Fruits/m <sup>2</sup>	
	Mean	Range
1995~1996	116	9~456
1997~1998	103	3~332

There were differences of fruit productions between each treatment and its control (Table 3), however, not significant. Fruit fall both in open plots and in closed plots with 4 × 4m<sup>2</sup> meshes also peaked in mid-December (Fig. 2).

*Phoebe bournei* apparently had no live seed in seed bank during late June and Sept. in 1998. All seeds separated from soil samples were decayed.

Table 2 Fruit fall in plots with 2 × 2m<sup>2</sup> meshes based on data from 20 parent trees between 1997 and 1998

Dissemination type	Fruit type	Estimated fruit production × 10 <sup>4</sup> /hm <sup>2</sup>	%
Directly fallen fruits	Intact fruits	1022.551	90.1
Bird-disseminated fruits	Seeds from dehiscing mature fruits	108.005	9.5
	and seeds defecated by birds		
Fruits attacked before dispersal	Exocarps pierced by a hole(s)	4.500	0.4
Total		1135.056	100.0

**Table 3 Fruit fall in plots with different treatments between 1997 and 1998**

Treatments	Fruits/m <sup>2</sup>	d/f	F	P
Plots with 2×2mm <sup>2</sup> meshes (Control)	103			
Plots with 4×4cm <sup>2</sup> meshes	116	1	6.8×10 <sup>-2</sup>	NS
Open plots	105	1	9.8×10 <sup>-1</sup>	NS

NS=not significant

fleshes of some fruits were still fresh.

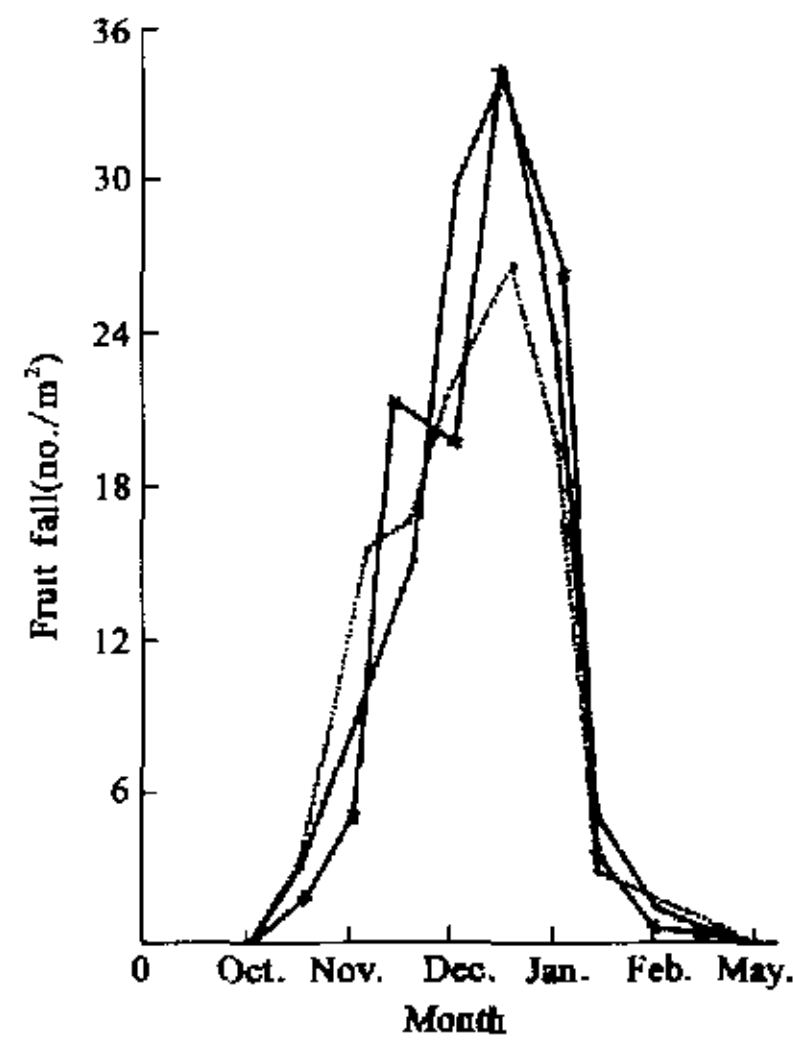


Fig. 2 Fruit fall in plots of three treatments between 1997 and 1998.

1. plots with 2×2mm<sup>2</sup> meshes (• and ...) 2. Open plots (... ) and 3. plots with 4×4cm<sup>2</sup> meshes (× and ...)

Field and laboratory germination rate differed sharply (Fig. 4). Laboratory germination rate was about 93 per cent compared to 12 per cent field germination rate. Poor field germination rate was mainly due to rotted seeds caused by high humidity. Based on data from 1000 fruits collected from plots, 385 fruits were rotted while

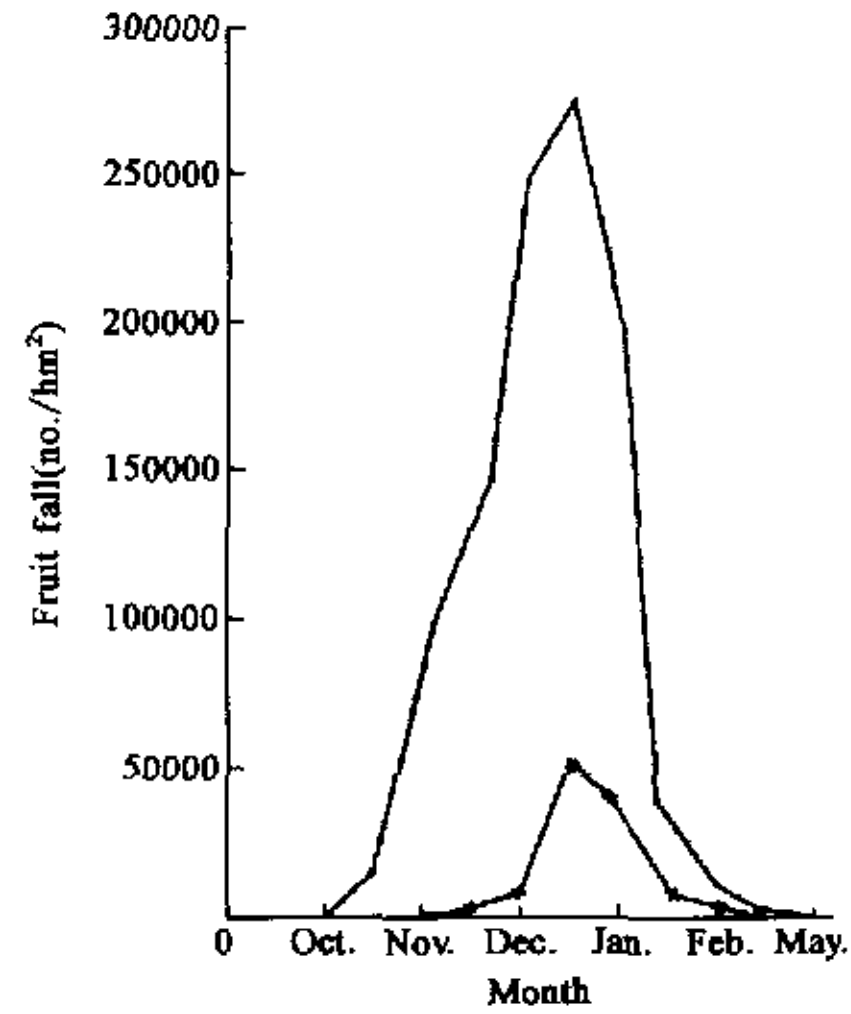


Fig. 3 Seasonal change of fruit-dissemination rate of directly fallen fruits (• and ...) and bird-disseminated fruits (× and ...) between 1997 and 1998

#### 4.2 Fruit/seed and seedling predation

The number of removed fruits in the unprotected plots differed significantly from that in the protected plots (Table 4). Predators removed averagely 57.2 per cent of monitored fruits in the unprotected plots during the study, however, removal rate varied wildly from 34.0 to 97.0 per cent. The number of eaten fruits in the protected plots was very low (less than 1.0 per cent), but fruits were frequently attacked by soil pathogens. The number of predated seedlings in the unprotected plots showed a significant difference from that in the protected plots (Table 4). 47.0 per cent of monitored seedlings were predated in the unprotected plots. Less than 10 per cent of seedlings in the protected plots were eaten by insects.

Fruits with high density showed low predation tendency, but no significant difference from those with low density (Table 5). Seedlings with high density suffered significantly higher mortality than those with low density within 2 months, but after 2 months, the difference was vague (Table 5). More than 90 per cent of fruits with low density were removed while about 87 per cent of fruits with high

**Table 4 F ratios and significance levels from analyses of variance of fruit or seedling loss with the treatment of protection**

Source	Treatment	d/f	F	P
Fruit	Protected	1	23.3	***
Seedling	Protected	1	102.2	***

\*\*\* P<0.001

density lost. 85 per cent of seedlings with low density were dead, due to all cases but physical damage, compared to 40 per cent with high density within 2 months after germination.

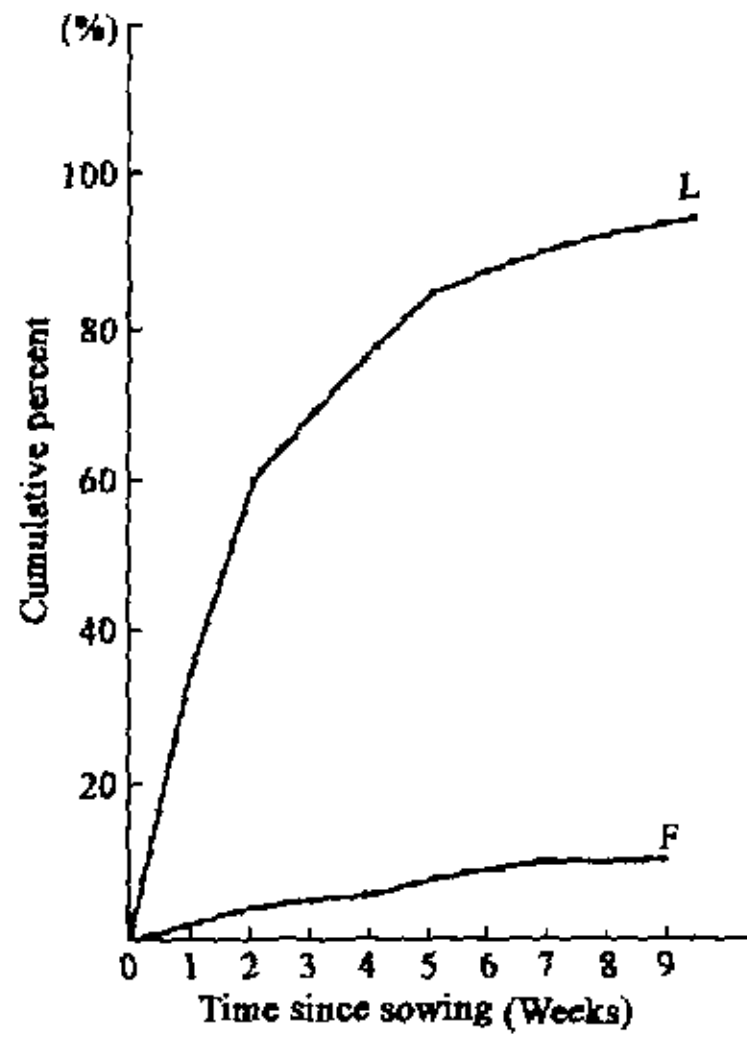


Fig. 4 Cumulative percent germination vs. time since sowing, based on field(F) and lab(L) trials in 1998

compared to 50 per cent in the plots far from parent trees. In forest gaps, fruit removal rate in the plots close to parent trees averaged 80 per cent compared to 45 per cent in the plots far from parent trees. The interaction between distance and canopy was, however, not significant (Table 6).

**Table 6** *F* ratios and significance levels from analyses of variance of fruit or seedling loss with treatments of canopy vs. gap(CG), far vs. near (FN) and their interaction (CG×FN)

Source	Treatments	df	<i>F</i>	<i>P</i>
Fruit	CG	1	24.1	***
	FN	1	602.1	***
	CG×FN	1	2.7	NS
Seedling	CG	1	48.8	***
	FN	1	120.4	***
	CG×FN	1	24.7	***

\*\*\*  $P < 0.001$ , NS = not significant

mortality rate in the plots close to parent trees was 89 per cent compared to 67 per cent in the plots far from parent trees. In forest gaps seedling mortality rate in the plots close to parent trees averaged 78 per cent compared to 2 per cent in the plots far from parent trees. The interaction between distance and canopy was significant (Table 6).

#### 4.3 Neighborhood interference among seedlings

1350 seedlings in all were counted and marked. Of which 4.3 per cent seedlings died due to damping off, herbivory and unknown factors. The data of physical damage were dropped from the analysis because physical damage was obviously irrelevant to neighborhood effect. The death number increased with the number of seedlings within distribution distance. The spatial distribution of seedlings showed an aggregat-

**Table 5** *F* ratios and significance levels from analyses of variance of fruit or seedling loss with treatment of density

Source	Time	Df	<i>F</i>	<i>P</i>
Fruit	Oct. ~ Mar.	1	3.5	NS
Seedling	Apr. ~ Jun.	1	24.8	**
Seedling	Jun. ~ Sep.	1	3.9	NS

\*\*  $P < 0.01$ , NS = not significant

Fruits beneath forest canopy suffered significantly higher predation than those in forest gaps (Table 6). In the plots close to parent trees, fruit removal rate beneath forest canopy averaged 90 per cent compared to 80 per cent in gaps. In the plots far from parent trees, fruit removal rate beneath forest canopy averaged 50 per cent compared to 45 per cent in gaps. Fruits in the plots far from parent trees suffered significantly lower predation than those in the plots close to parent trees (Table 6). Beneath forest canopy, fruit removal rate in the plots close to parent trees was 90 per cent com-

pared to 50 per cent in the plots far from parent trees. In forest gaps, fruit removal rate in the plots close to parent trees averaged 80 per cent compared to 45 per cent in the plots far from parent trees. The interaction between distance and canopy was, however, not significant (Table 6). Seedlings beneath forest canopy suffered significantly higher mortality than those in forest gaps (Table 6). In the plots close to parent trees, seedling mortality rate beneath forest canopy averaged 89 per cent compared to 78 per cent in gaps. In the plots far from parent trees, seedling mortality rate beneath forest canopy averaged 67 per cent compared to 2 per cent in gaps. Seedlings in the plots far from parent trees suffered significantly lower mortality than those in the plots close to parent trees (Table 6). Beneath forest canopy, seedling



ed pattern. There were 482 pairs of seedlings with the distance between them  $\leq 5\text{cm}$  and 12 per cent of them died.

## 5 Discussion

Oily fruits or fruits with bicolor display attract migrating birds<sup>[14]</sup>. A time lag between fruiting phenology and the presence of migratory birds is, however, contradictory to the concept<sup>[11]</sup>. Because seeds defecated by birds and seeds from dehiscing mature fruits coincided in this study design, the actual number of bird disseminated fruits and thus its peaking time can not be known. Whether a lag time existed or not remains unclear in this study. However, we suspect a lag time actually existed because only less than 10 per cent of fruits were disseminated by birds. Seeds could be carried beyond parent tree's canopy by birds. But traps were beneath parent tree's canopy in the study. So the number of bird-disseminated fruits is not complete when distance is considered. However, Spatial patterns around parent trees show that both density of directly fallen fruits and bird-disseminated fruits decrease with distance from a mature trees<sup>[15]</sup>. Furthermore, the study of seed passage showed that predicted median dispersal distance increases dramatically with increasing retention time in bird guts only in a very short time, but slightly thereafter<sup>[1]</sup>. Although we could not figure out how long birds perched on parent trees, yet *Phoebe* dominant communities in LNR, ranging generally from 5 000m<sup>2</sup> to 8 000m<sup>2</sup>, are large to the extent to be of interest to birds. Thus, as we documented in this study, most fruits were disseminated by gravity, not by birds. However, further studies are still required to clarify bird dissemination.

Climax or non-pioneer species<sup>[11]</sup> tend to have larger seeds with little dormancy, and rapid germination following dispersal<sup>[32]</sup>. For *Phoebe*, seeds germinated in early April and were inviable after July, showing no persistent seed bank strategy. In viable fruits in the field usually mould. Beneath forest canopy, fruits of *Phoebe* were easy to suffer soil pathogens, contrary to in forest gaps with higher light and lower humidity inimical to plant pathogens. Especially, large gaps in LNR were rare and most fruits were beneath forest canopy, so fruits were frequently attacked by soil pathogens. The situation was exacerbated by high moist habitats. In addition, only 12 per cent fruits germinated in the field, compared to as high as  $\approx 93$  per cent in laboratory. Poor field germination rate was also mainly due to soil pathogen attack. So further work with *Phoebe* regeneration, which may cause this species to be rare and endangered, should focus on pathogens responsible for low germination rate.

Many studies found seedling survival was greater in gaps than in the understory<sup>[8]</sup>. *Phoebe* seed survival was higher in forest gaps, probably because of, however, not only higher light level and lower humidity, but more danger and fewer resources to frugivores as well. Furthermore, low level of fruit or seedling predation was a more important determinant of high seed or seedling survival than was light level or moisture condition. This is consistent with the study of Sork<sup>[33]</sup> on *Gustavia* that mammalian predation on seedlings was more important than light conditions in determining its seedling density.

Effect of predators on seed or seedling survival is usually studied by the treatment of closed plots vs. open plots<sup>[7]</sup>. Although fruits in unprotected plots suffered significantly higher predation than those in protected plots (Table 4), yet fruits in open plots and closed plots with 4 × 4cm<sup>2</sup> meshes showed no significantly higher predation than those in closed plots with 2 × 2mm<sup>2</sup> meshes (Table 3). The most possible cause is that the position of a plot beneath a parent tree's canopy may affect fruit collection due to different flowering branches. In the study, fruit production varied wildly from 3 to 332 fruits/m<sup>2</sup> in closed plots with 2 × 2mm<sup>2</sup> meshes. In addition, removal of fruits into open plots or plots with 4 × 4cm<sup>2</sup> meshes by insects, animals or birds also made this possible.

In this study we considered damping-off, herbivory and unknown case to be the result of neighbor-



hood effect, because neighborhood effect can be caused by density-responsive natural enemies<sup>[22]</sup>. The model showed that density dependent mortality of seedlings occurred during the first 3 months. Furthermore, seedlings with high density suffered significantly higher mortality than those with low density within 2 months (Table 5). The results are consistent with many recent studies<sup>[26]</sup>. However, fruits with high density did not suffered significantly lower predation than those with low density (Table 5). Strong<sup>[27]</sup> discussed the concept of "density vagueness", which implies that density-dependence acts only at very low or very high population levels. It seems that *Phoebe* density-dependence occurred conditionally too. In species-rich communities such as tropical forests, near neighbors are seldom conspecific<sup>[38]</sup>, and the density of even the most abundant species is nowhere near the "self-thinning" density. But in mid-subtropical evergreen broadleaf forest, conspecific neighbors occur frequently in communities dominated by one or two species. In *Phoebe* dominant communities, *Phoebe* was so abundant, partly due to polyembryony, that individuals of this species were usually close neighbors of conspecifics. Especially fallen fruits often aggregate around parent trees and after germination neighborhood effect of seedlings arises. Many studies have shown declines in seed and seedling survival of tropical trees in regions close to adults, or in regions of high seed or seedling density<sup>[23,25]</sup>. Howe *et al.*<sup>[26]</sup> and Augspurger<sup>[2,1]</sup> demonstrated reduction of seedling survival as far as 25~50m from conspecific adults in a tropical tree species. These studies showed that wide seed dispersal could be considered as one of the mechanisms for escaping from such high mortality in sites near the parents or with high density. We did not figure out how far fruits were disseminated and how many fruits were disseminated to far distance in this study. However, most *Phoebe* fruits or seedlings may be beneath parent tree's canopy or within near distance, so density dependent mortality occurred frequently, though only at the early seedling stage.

All in all, high environment pressures on seed and seedling of *Phoebe bournei* place an obstacle to the survival of this species, which, we consider, is one of the most important causes to threaten this species.

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