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ORIGINAL ARTICLE

Fluctuation in seed abundance has contrasting effects on the fate of seeds from two rapidly germinating tree species in an Asian tropical forest

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Abstract

The seed predator satiation hypothesis states that high seed abundance can satiate seed predators or seed dispersers, thus promoting seed survival. However, for rapidly germinating seeds in tropical forests, high seed abundance may limit dispersal as the seeds usually remain under parent trees for long periods, which may lead to high mortality due to rodent predation or fungal infestations. By tracking 2 species of rapidly germinating seeds (*Pittosporopsis kerrii*, family Icacinaceae; *Camellia kissi*, family Theaceae), which depend on dispersal by scatter-hoarding rodents, we investigated the effects of seed abundance at the community level on predation and seed dispersal in the tropical forest of Xishuangbanna Prefecture, Southwest China. We found that high seed abundance at the community level was associated with delayed and reduced seed removal, decreased dispersal distance and increased pre-dispersal seed survival for both plant species. High seed abundance was also associated with reduced seed caching of *C. kissi*, but it showed little effect on seed caching of *P. kerrii.* However, post-dispersal seed survival for the 2 plant species followed the reverse pattern. High seed abundance in the community was associated with higher post-dispersal survival of *P. kerrii* seeds, but with lower post-dispersal survival of *C. kissi* seeds. Our results suggest that different plant species derive benefit from fluctuations in seed production in different ways.

Key words: predator satiation, rapidly germinating seeds, scatter-hoarding, seed abundance, seed dispersal

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INTRODUCTION

The seed predator satiation hypothesis states that high seed abundance during mast-seeding years can satiate seed predators under parent trees and benefit pre-dispersal seed survival (Janzen 1971; Silvertown 1980; Sork 1993; Kelly 1994). Some studies have also found that mast seeding can benefit plants by attracting seed dispersers when a large seed crop is produced, because seeds can then be removed more rapidly and dispersed further; this is referred to as the animal-mediated dispersal hypothesis (Kelly 1994; Kelly & Sork 2002). For plants predominately dispersed by scatter-hoarding rodents, predicting the consequence of seed fate is complex, because scatter-hoarding rodents are both predators and dispersers. In recent years, many studies have investigated the effects of mast seeding on seed dispersal by scatter-hoarding rodents (Hoshizaki & Hulme 2002; Vander Wall 2002; Jansen *et al.* 2004; Xiao *et al.* 2005, 2013c; Li & Zhang 2007; Zhang *et al.* 2008; Fletcher *et al.* 2010; Yi *et al.* 2011; Lai *et al.* 2014). One of those studies found that seeds experienced a more rapid harvest, greater dispersal distance and higher post-dispersal seed survival in mast-seeding years (Vander Wall 2002), which was predicted by the animal-mediated dispersal hypothesis (Kelly 1994). However, in other studies, mast seeding was more likely to represent a strategy to increase seed survival by satiating seed predators (Jansen *et al.* 2004; Xiao *et al.* 2005, 2013c), rather than attracting seed dispersers to accomplish seed dispersal. Those studies found that in mast-seeding years, seeds experienced slower removal, lower seed caching and shorter dispersal distances than in non-mast seeding years (Jansen *et al.* 2004; Xiao *et al.* 2013c). Some of those studies also found that post-dispersal seed survival was higher during mast-seeding years (Jansen *et al.* 2004); however, one long-term study showed that mast seeding increased pre-dispersal seed survival but reduced post-dispersal seed survival (Xiao *et al.* 2013c).

Seed predator satiation is determined by seed abundance at the population level and is also affected at the community level, because high seed abundance at the community level has a significant effect on seed dispersal and survival (Hoshizaki & Hulme 2002; Xiao *et al.* 2005, 2006b). This may be because seed predators or dispersers, such as rodents, are usually generalists; that is, one rodent species may predate and disperse many species of plant seeds (Vander Wall 1995; Chang & Zhang 2014; Wang *et al.* 2014). Thus, seed predation and seed dispersal of a given plant species can be affected by another plant species (Yi *et al.* 2011; Lichti *et al.* 2014). To date, few studies have investigated how seed abundance at the community level affects seed dispersal and survival in non-mast-seeding plants.

High seed abundance may have unforeseen negative consequences; for example, seed-predator or seed-disperser satiation is usually accompanied by slower seed removal, shorter dispersal distance, and decreasing probability of seed removal and caching (Jansen *et al.* 2004; Xiao *et al.* 2013c). For large-seeded tropical plant species, which depend on dispersal by scatter-hoarding animals, this could be a particular disadvantage as they tend to germinate rapidly after ripening. In this situation, seeds will be exposed to seed predators or fungi for a longer time before they encounter seed dispersers, or seeds will germinate and seedlings will establish under parent trees (Chapman & Chapman 1995; Cao *et al.* 2011b). Growing evidence indicates that seed perishability may affect the predation and hoarding behavior of scatter-hoarding rodents (Hadj-Chikh *et al.* 1996; Steele *et al.* 2006; Xiao *et al.* 2009, 2010, 2013b). In addition, there is evidence that scatter-hoarding rodents are more likely to predate non-dormant seeds immediately, as well as cached dormant seeds. They are also more likely to remove the embryos of non-dormant seeds prior to hoarding for use as a long-term food reserve (Steele *et al.* 2001; Xiao *et al.* 2013a,b). It is possible that fluctuations in seed abundance interact with the characteristics of early seed germination, which then affects seed dispersal and plant regeneration. However, how seed abundance at the community level affects the fate and dispersal of rapidly germinating seeds in tropical rain forests remains unclear.

In this study, we investigated the effects of seed abundance at the community level on the dispersal of 2 species of rapidly germinating seeds (*Pittosporopsis kerrii* and *Camellia kissi*, both non-mast seeding plants) dispersed by scatter-hoarding rodents in tropical forests in Xishuangbanna, China. We test the following 2 hypotheses: (1) high seed abundance at the community level could satiate seed predation by scatter-hoarding rodents and increase pre-dispersal seed survival, as predicted by the seed predator satiation hypothesis; (2) high seed abundance could reduce post-dispersal seed survival of rapidly germinating seeds, as slower seed removal increases the number of seeds eaten by rodents or infested by fungi and thereby reduces the success of seed dispersal.

MATERIALS AND METHODS

Study site and study species

The study was carried out in a tropical montane evergreen broad-leaf forest of the Menglun Nature Reserve (21°50′N, 101°12′E, elevation 780 m), Xishuangbanna Prefecture, Yunnan Province, China. The average annual rainfall is approximately 1500 mm, with 80% falling during the wet season (May–October) and 20% falling in the dry season (November–April) (Cao & Zhang 1997). The forest is dominated by *Castanopsis echidnocarpa*, *Aporusa yunnanensis*, *Olea rosea*, *Lithocarpus truncates*, and *Schima wallichii* (Zhang & Cao 1995).

The focal plants of this study were *P. kerrii* (Icacinaceae) and *C. kissi* (Theaceae). *P. kerrii* is the dominant plant species (shrub or small tree) in the tropical rainforests of Xishuangbanna (Lan *et al.* 2008), and it is a common species in tropical montane evergreen broad-leaved forests. The fruit of *P. kerrii* is a drupe (fresh fruit mass was 7.14 ± 1.65 g, $n = 98$, mean ± SD). It contains a large seed (fresh seed mass was 5.58 ± 1.40 g), and ripens between August and September. No animals were observed consuming the pulp, which usually decomposes quickly after falling to the ground. *C. kissi* is also a common plant species (shrub or small tree) in the tropical montane evergreen broad-leaved forest of Xishuangbanna. *C. kissi* usually produces a capsule fruit, which ripens between July and September. Each fruit contains 1–6 seeds (fresh seed mass was 1.58 ± 0.20 g). Seeds of both species germinate quickly after falling to the ground. We observed that 99% of *P. kerrii* ($n = 50$) seeds germinated within 2 weeks after being buried in the soil (Cao *et al.*, unpubl. data), and many *C. kissi* seeds germinated within 2–4 weeks of falling to the ground (L. Cao, pers. observ.). Rodents were observed pruning protruding radicles (of *P. kerrii*) or removing embryos (of *C. kissi*) when caching seeds. The seeds of *P. kerrii* have a high regeneration capacity; both pruned seeds and pruned radicles retain the ability to develop into seedlings (Cao *et al.* 2011b). The seeds of *C. kissi* are less resilient; seeds with the embryo removed could not germinate. These 2 species of plants produced fruit every year for 8 years (2007–2014, L. Cao, pers. observ.), and did not show significant mast seeding as displayed by strictly mast-seeding plants or by some normal mast-seeding plants.

At the study site, *Niviventer confucianus* (Milne-Edwards, 1871) is the dominant rodent species; *Niviventer fulvescens* (Gray, 1847), *Maxomys surifer* (Miller, 1900) and *Rattus flavipectus* (Temminck, 1844) are also commonly seen. Three of these species (*N. confucianus*, *N. fulvescens* and *M. surifer*) have been noted for their scatter-hoarding behavior and act as important seed dispersers for many large-sized seeds in the Xishuangbanna tropical forest (Cao *et al.* 2011a,b; Wang *et al.* 2014).

Seed crop and rodents abundance

We measured seed crops in the community using 110 seed traps (0.5-m^2-sample area, placed 1 m above the ground) in the study site in 2007 and 2008. Seed traps were placed in 3 plots (50 traps were placed in 1 plot, and 30 traps were placed in the other 2 plots) approximately 200 or 500 m away from a seed-releasing experimental stand, spaced approximately 10 m apart in 2 lines, without considering which trees seed traps were placed underneath. In this way, we could monitor seed crops within the community. Seeds contained in the traps were counted every 2 or 4 weeks from August to March of the following year. As few *P. kerrii* and *C. kissi* seeds were collected in the traps, we also measured the seed crop of *P. kerrii* in 2008 (failed in 2007, seed crops of 67 individual plants were measured in 2008) by counting fruits on the plants. In addition, the seed crop of *C. kissi* was measured in 2007 and 2008 by collecting all fruits from the fruiting plants (seed crops of 18 *C. kissi* individual plants were measured; however, 3 plants marked in 2007 were not retrieved in 2008).

We estimated the relative abundance of rodents in September and December in 2007 and 2008 near to the stand from where the seed releasing experiments were conducted. We selected 2 plots for trapping rodents. In each plot, we set a 5 × 10 trapping grid (spaced 10 m apart), which consisted of 50 live traps (L × W × H = 14 cm × 14 cm × 30 cm; our own design was approved by the Institute of Zoology, Chinese Academy of Science), which were baited with fresh peanuts following the methods described by Chang et *al.* (2009). Trapping was conducted for 3 consecutive days in September and December in 2007 and 2008 for each plot (150 trap days for each trapping time). Captured rodents were identified, weighed, marked (individual rodents were marked using colored paint to permit identification during the survey) and released immediately *in situ*.

Seed releasing experiments

We tracked the fate of *P. kerrii* and *C. kissi* seeds at the study site in 2007, which was a year of low seed abundance at the community level, and in 2008, which was a year of high seed abundance at the community level. For each year, 540 intact *P. kerrii* seeds and 400 intact *C. kissi* seeds were used for the seed-releasing experiments. Each seed was labeled with a small coded plastic tag attached through a 16-cm thin steel thread (Xiao *et al.* 2006a). This method of tagging has a negligible effect on seed removal by rodents (Xiao *et al.* 2006a). However, the plastic tags may attract potential pilferers and, therefore, increase pilferage rates after caching; therefore, this method of tagging may reduce post-dispersal seed survival. We placed 18 seed stations

(30 seeds per station) spaced approximately 10–20 m apart along a single transect to track the fate of *P. kerrii* Craib seeds, and 8 seed stations (50 seeds per station) spaced approximately 40 m apart along the same transect to track the fates of *C. kissi* seeds. The nearest distance between seed stations of the 2 plants was approximately 200 m. The seed station was protected by a steel wire-mesh enclosure (enclosure size: 0.7 m × 0.7 m × 0.5 m; mesh size: 1 × 1 cm), with 1 small hole (10 × 10 cm) on each side of the 4 walls to allow access by rodents and to prevent access by large vertebrates such as *Sus scrofa*.

Tagged seeds of these 2 plants were released in late August or early September of each year. The fate of the tagged seeds was surveyed at weeks 2, 4, 8, 12 and 16 of the release year, and then in March, July or September of the following year. During each survey, we searched the area around each seed station to retrieve the tagged seeds and record the seed fate. Seed fate at each station was categorized as follows: eaten by rodents (consumed by rodents leaving only tags and seed fragments), eaten by ants, decomposed (infested by fungi), established (germinated and established seedling) and removed. Removed seeds were further categorized as cached (intact seeds buried in the surface soil or beneath leaf litters), eaten by rodents, or missing (fate unknown). For cached seeds or seed fragments, we recorded the distance from the seed stations. Cached seeds were marked using a numbered bamboo stick approximately 20 cm from the seeds. At subsequent visits, we checked the cached seeds located during previous visits until they were recovered (eaten or removed) by animals, eaten by ants or decomposed. If a marked cache was removed, the area around the cache was searched extensively. When cached seeds were removed and found re-cached at other caching sites, the seed fate and distance from seed stations was recorded. We surveyed all previous cache sites to determine whether the cached seeds established seedlings.

Data analysis

All statistical analyses were performed using SPSS Statistics 20.0. Seed survival time at the seed station (days until being eaten, removed, rotten, or established at seed station after releasing) was analyzed by the Cox regression model. Seed fate at seed stations, fate after removal, final fate and dispersal distance of 2 species plants between 2 years were analyzed using the Mann-Whitney *U*-test.

RESULTS

Seed crop and rodent abundance

We collected 47 seeds from 6 plant species in 2007, and 550 seeds from 8 plant species in 2008 (Table 1). The seed crops for all plant species collected in seed traps in 2007 (low seed abundance year) were lower than those in 2008 (high seed abundance year, Table 1). We found that *Lithocarpus truncates* and *L. leucostachyus* performed mast-seeding in 2008, but no plant species performed mast-seeding in 2007.

The mean crop size for *P. kerrii* consisted of 5.2 ± 15.1 seeds (varying from 0 to 117 seeds, $n = 67$ individual plants) per plant in 2008. The mean crop size for *C. kissi* was 113.1 ± 168.1 seeds (varying from 9 to 704 seeds, $n = 18$ individual plants) per plant in 2007, and 112.1 ± 121.8 seeds (varying from 10 to 431 seeds, $n = 15$ individual plants) per plant in 2008.

We captured 27 individual animals representing 3 rodent species in 2007 and 7 individual animals representing 3 species in 2008 (Table 2). In 2007, the trap was

Table 1 Seed crop of plant species depended on dispersal by scatter-hoarding animals in 2007 and 2008, respectively (seed number/m^2, $n = 110$ traps for each year)

Species	2007 (Mean ± SD)	2008 (Mean ± SD)
Castanopsis echinocarpa	0.02 ± 0.19	2.88 ± 10.84
Castanopsis calathiformis	0.35 ± 3.62	0.85 ± 6.92
Castanopsis indica	0.02 ± 0.19	0.17 ± 0.77
Lithocarpus truncatus	0.09 ± 0.95	4.38 ± 26.97
Lithocarpus leucostachyus	0.34 ± 2.64	1.58 ± 8.96
Lithocarpus magneinii	0	0.06 ± 0.33
Pittosporopsis kerrii	0.04 ± 0.38	0.07 ± 0.76
Camellia kissi	0	0.02 ± 0.19
Total	0.85 ± 4.55	10 ± 32.95

Table 2 Number of rodents captured in 2007 and 2008 (600 capture nights for each year)

Rodent species	2007	2008
Niviventer confucianus	25	5
Niviventer fulvescens	1	1
Maxomys surifer	1	0
Leopoldamys edwardsi	0	1

almost 4 times more successful than in 2008 (4.5% *vs* 1.17%, respectively).

Seed dispersal and survival

Tagged seeds from both plant species were quickly harvested (eaten or removed) in 2007, while most seeds remained at seed stations for longer in 2008 (Fig. 1). The seed survival time at seed stations in 2007 was shorter for both plant species than in 2008 (*P. kerrii*, Wald = 382.4, df = 1, $P < 0.001$; *C. kissi*, Wald = 355.5, df = 1, $P < 0.001$).

In both years, most *P. kerrii* seeds were removed from seed stations by rodents (Table 3); and although most *C. kissi* seeds were removed in 2007, only 21% were removed in 2008 (Table 3). The proportion of removed seeds was higher in 2007 than in 2008 for both plants (*P. kerrii*, $U = -3.734$, $P < 0.001$; *C. kissi*, $U = -3.361$, $P = 0.001$; Table 3). The proportion of *P. kerrii* seeds eaten by rodents at seed stations did not differ significantly between the 2 years ($U = -1.205$, $P = 0.228$; Table 3), although more *C. kissi* seeds were eaten by rodents in 2008 than in 2007 ($U = -2.31$, $P = 0.021$; Table 3). The proportion of seeds that rotted at seed stations was higher in 2008 than in 2007 for both plant species (*P. kerrii*, $U = -3.237$, $P = 0.001$; *C. kissi*, $U = -2.962$, $P = 0.003$; Table 3). Overall, 12.6% of *P. kerrii* seeds and 2.5% of *C. kissi* seeds survived as established seedlings in 2008 at seed stations (Table 3), but no seeds for either species survived as establish seedlings in 2007 at seed stations.

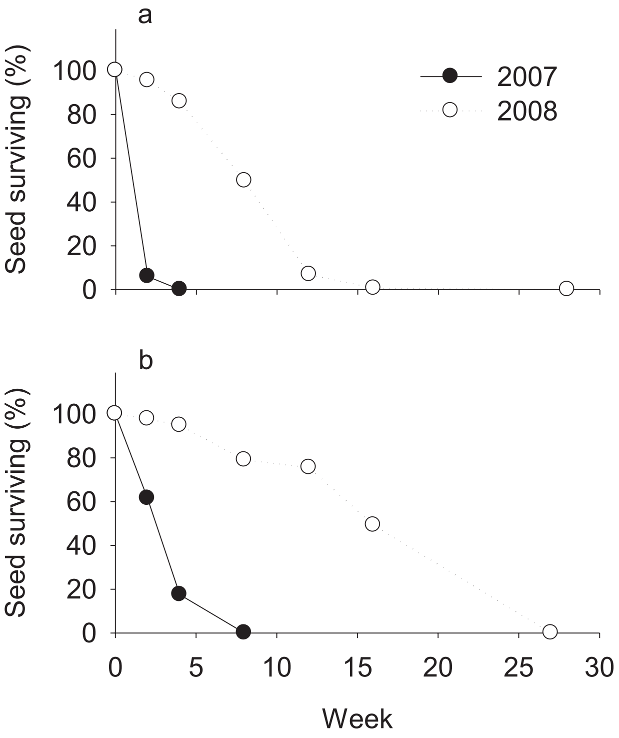

Figure 1 Survival curve (proportion) of tagged seeds after placement at seed stations: (a) *Pittosporopsis kerrii* and (b) *Camellia kissi.*

Table 3 Seed fates at seed stations or after removal. Proportion (mean ± SE) of seeds removed or eaten by rodents, eaten by ants, rotten or establish seedlings at seed stations; and proportion of seeds in primary, secondary and tertiary caches

	Pittosporopsis kerrii		*Camellia kissi*	
Seed fate	2007	2008	2007	2008
Fates at seed stations				
Removed from seed stations	98.7 ± 0.5	76.8 ± 4.5	76.2 ± 5.4	21 ± 5.6
Eaten by rodents	1.1 ± 0.5	4.4 ± 2.2	1.5 ± 0.7	35.7 ± 9.1
Eaten by ants	0	0	21.7 ± 5.2	17.7 ± 7.6
Rotten	0.2 ± 0.2	6.1 ± 2.5	0.5 ± 0.3	23 ± 10.2
Seedling establishment at stations	0	12.6 ± 3.8	0	2.5 ± 1.7
Fates after removal				
Primary caches	32.0 ± 4.3	22.8 ± 3.9	48.5 ± 7.4	5 ± 2.5
Secondary caches	1.3 ± 0.7	0.7 ± 0.4	13.7 ± 6.1	0
Tertiary caches	0	0	2 ± 5.6	0
Seedling establishment after removal	0	2.2 ± 0.4	0.8 ± 0.6	0

After seeds were removed from seed stations, we found that the proportion of *P. kerrii* seeds scatter-hoarded (primary caches) by rodents did not differ significantly between the 2 years ($U = -1.587$, $P = 0.112$; Table 3); however, the proportion of scatter-hoarded *C. kissi* seeds (primary caches) in 2007 was significantly higher than in 2008 ($U = -3.414$, $P = 0.001$; Table 3). Most seeds in primary caches were recovered by rodents, regardless of the species. A few *P. kerrii* seeds were re-cached (secondary cache, Table 3); and approximately 13.7% ($n = 55$) of the *C. kissi* seeds were in secondary cache in 2007; however, no seeds were in secondary cache in 2008 (Table 3). Apart from 2% of *C. kissi* seeds in 2007, no other seeds were observed in the tertiary cache in 2008 (Table 3). Rodents were observed pruning the protruding radicle of *P. kerrii* seeds and removing the embryo of *C. kissi* seeds during caching. A total of 13.4% ($n = 45$) and 39.4% ($n = 121$) of *P. kerrii* seeds were in primary caches, which were observed to be pruned of the protruding radicles in 2007 and 2008, respectively; all of the *P. kerrii* seeds in secondary caches were observed to be pruned in both years. Only 5 *C. kissi* seeds were observed with their embryos removed in both years.

In total, 12 (2.2%) *P. kerrii* seeds survived and established seedlings after removal (post-dispersal seedling establishment) in 2008, and no seeds established seedlings in 2007 after removal. All seedlings from removed *P. kerrii* seeds were from primary caches, and 9 were established from radicle-pruned seeds or pruned radicles. Three *C. kissi* seeds (0.8%) survived to establish seedlings after removal in 2007, but no seeds established seedlings in 2008 after removal.

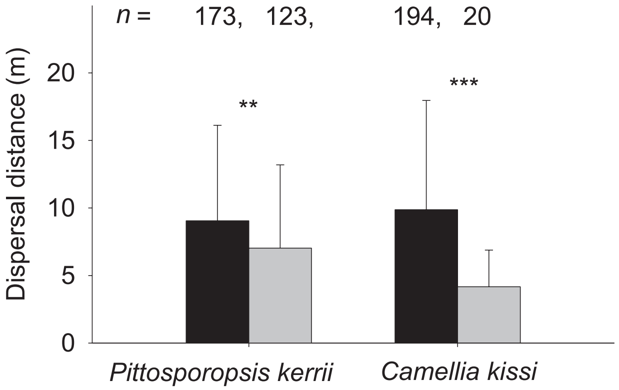

Figure 2 Seed dispersal distance of primary cache (mean ± SD) of *Pittosporopsis kerrii* and *Camellia kissi* seeds in 2007 (black bar) and 2008 (grey bar). Mann–Whitney U-test, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Dispersal distance

The mean dispersal distance of *P. kerrii* seeds was 9.0 ± 7.1 m (mean ± SD, $n = 173$, from 0.3 to 30.4 m) and 7.0 ± 6.2 m ($n = 123$, from 0.4 to 34 m) in 2007 and 2008, respectively (Fig. 2); while the mean dispersal distance of *C. kissi* seeds was 9.9 ± 8.1 m ($n = 194$, from 0.4 to 70.2 m) and 4.2 ± 2.7 m ($n = 20$, from 1.4 to 14.5 m) in 2007 and 2008 respectively (Fig. 2). The mean dispersal distances for both plant species in 2007 were significantly greater than those in 2008 (*P. kerrii*, $U = -2.929$, $P = 0.003$; *C. kissi*, $U = -3.979$, $P < 0.001$).

DISCUSSION

Our results showed that high seed abundance in the community was associated with delayed and reduced seed removal, decreased dispersal distance, and increased pre-dispersal seed survival (seedling establishment) for both plant species. High seed abundance was also associated with reduced seed caching of *C. kissi*, but it had little effect on seed caching of *P. kerrii*. However, the reverse effect was observed for high seed abundance on post-dispersal seed survival for the 2 plant species, such that high seed abundance was associated with higher post-dispersal survival of *P. kerrii* seeds but lower post-dispersal survival of *C. kissi* seeds.

The predator satiation hypothesis states that high seed abundance can promote pre-dispersal seed survival by reducing seed losses from seed predators (Janzen 1971; Silvertown 1980; Sork 1993; Kelly 1994). This has been supported by the findings of many studies (Silvertown 1980; Sork 1993; Kelly & Sork 2002; Kon *et al.* 2005; Xiao *et al.* 2013c). It is unclear whether high seed abundance promotes post-dispersal seed survival of predator-dispersed plants. Some studies have found that high seed abundance can promote post-dispersal seed survival of those plants dispersed by scatter-hoarding rodents (Vander Wall 2002; Jansen *et al.* 2004); however, Xiao *et al.* (2013c) found seed abundance to be negatively correlated with post-dispersal seed survival. In the present study, we found a contradictory result for the effect of high seed abundance on post-dispersal seed survival.

Mast-seeding or high seed abundance was not necessarily beneficial to post-dispersal seed survival. Post-dispersal seed survival requires seeds to survive in order to establish seedlings, but it also requires seeds to be removed and cached far from their parent trees. Mast-seeding or high seed abundance is usually accompanied by delayed and reduced seed removal and caching (Jansen *et al.* 2004; Xiao *et al.* 2005, 2013c), and may ultimately reduce post-dispersal seed survival (Xiao *et al.* 2013c).

Remaining under parent trees may be disadvantageous to seed dispersal for some plant species over the long term (Xiao *et al.* 2013c). In this study, delayed removal of *C. kissi* seeds in a high seed abundance year (2008) resulted in more seeds rotting, being eaten by rodents, or establishing seedlings at seed stations; thus, very few seeds were removed and cached, subsequently reducing post-dispersal seed survival. In contrast, many *P. kerrii* seeds were removed and cached in a high seed abundance year, even though many seeds still rotted or established seedlings at seed stations. The seed perishability hypothesis proposes that rapidly germinating seeds are more likely to be predated immediately or have their embryo removed prior to hoarding. Several species of rodents have been observed to remove embryo or prune the protruding radicles of germinating seeds (Jansen *et al.* 2006; Steele *et al.* 2001, 2006; Xiao *et al.* 2009, 2013a,b; Cao *et al.* 2011b). Here, we also found that rodents frequently pruned protruding radicles of germinating *P. kerrii* seeds prior to hoarding in low and high seed abundance years. In this way, the rodents could also use germinating seeds as a long-term food reserve (Cao *et al.* 2011b). Because the high regeneration capacity of *P. kerrii* seeds helps radicle-pruned seeds to germinate and establish seedlings (Cao *et al.* 2011b), we found that many *P. kerrii* seeds established seedlings following removal during the high seed abundance year. Instead, we found that rodents preferred to consume germinating *C. kissi* seeds directly from seed stations; therefore, few seeds were cached and survived during the high seed abundance year.

Seed dispersal is a complicated process (Lichti *et al.* 2015), which is usually affected by many factors, such as seed abundance (Jansen *et al.* 2004; Xiao *et al.* 2005; Zhang *et al.* 2008), seed size (Forget *et al.* 1998; Jansen *et al.* 2002), nutrition (Vickery *et al.* 1994; Wang & Chen 2012), physical or chemical seed defenses (Smallwood & Peters 1986; Vander Wall 2001; Xiao *et al.* 2008; Zhang & Zhang 2008; Wang *et al.* 2014), other sympatric plants (Hoshizaki & Hulme 2002; Caccia *et al.* 2006; Yi *et al.* 2011; Lichti *et al.* 2014), and predation risks (Steele *et al.* 2014; Steele *et al*. 2015), and human disturbance (Zhang *et al.* 2016). These factors may interact, and could further affect seed dispersal and survival (Jansen *et al.* 2004; Wang & Chen 2012; Xiao *et al.* 2013a; Lichti *et al.* 2014). Therefore, it is necessary to assess the effects of other factors in order to understand the role of seed abundance on seed dispersal and survival at the population and community levels.

Rapid seed germination may require seeds to be removed as quickly as possible for successful seed dispersal, which seems to conflict with the effects of mast-seeding, which usually delays seed removal. Thus, it is possible that plant species that produce rapidly germinating seeds represent a trade-off between seed dispersal and producing a large number of seeds to satiate seed dispersers. Neither plant species in the present study exhibited mast-seeding during 8 years of observations (from 2007 to 2014, L. Cao, pers. observ.) at this study site. In a lowland rain forest in French Guiana, Jansen *et al.* (2004) also found that seed production of a rodent-dispersed tree *Carapa procera* (producing rapidly germinating seeds) in seed-rich years was only 22.9% higher than in seed-poor years. In contrast, seed crops in mast years are typically 100–1000 times larger than in non-mast years for some mast-seeding plants (see review by Vander Wall 2001). Xiao *et al.* (2013c) also suggested that mast-seeding plants that depend on dispersal by seed predators may trade off between seed dispersal and seed survival, because the net benefit of mast-seeding may depend on both the proportion of seeds surviving and the proportion of seeds dispersed far from the parent trees (Moore & Swihart 2007).

In conclusion, the results of our study demonstrate that high seed abundance at the community level can satiate seed predators and seed dispersers, thus benefitting pre-dispersal seed survival for both plant species. However, we found that the effects of high seed abundance on post-dispersal seed survival are complicated. High seed abundance in the community was associated with increased post-dispersal survival of *P. kerrii* seeds, but with reduced post-dispersal survival of *C. kissi* seeds. The results found for both plants supported hypothesis (1), such that high seed abundance at the community level satiated seed predation by scatter-hoarding rodents, and increased pre-dispersal seed survival of both plants. However, support for hypothesis (2) (that high seed abundance would reduce post-dispersal seed survival) from these findings was mixed; the fate of *C. kissi* seeds supported this hypothesis but the results for *P. kerrii* did not. Our results suggest that different plant species can derive benefit in different ways during years of low and high seed abundance.

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