兽类学报，2011，31（4）：323－329
Acta Theriologica Sinica

Effectiveness of small rodents dispersing seeds of *Castanopsis indica* in Xishuangbanna tropical seasonal rain forest

CAO Lin[1,2], GUO Cong[1*]

(1 Key Laboratory of Bio-resources and Eco-environment, Ministry of Education, College of Life Science, Sichuan University, Chengdu 610064, China)

(2 State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China)

Abstract: The effectiveness of *Castanopsis indica* seed dispersal was studied in the tropical rain forest in the Xishuangbanna region, Yunnan Province, China. We experimentally tracked the fate of 600 tagged nuts of *C. indica* under three focal trees (200 nuts for each tree) each year from November 2007 to November 2009. We investigated the proportion of experimental nuts moved away from the seed stations, the proportion of cached nuts buried beneath leaf litter or in soil, the number of nuts per cache, the distance that nuts were transported, and finally the proportion of nut surviving after being removed by rodents. Our results show that 69.3% of the tagged *C. indica* nuts under focal trees were dispersed by rodents, 18% of which were cached. All cached nuts were buried beneath leaf litter or in soil, and most caches contained only one nut, which may benefit nuts germination and seedling establishment. The dispersal distance of cached nuts averaged 7.1 m, ranging from 0.5 to 43.8 m, and there was no significant difference in distance variation among these three years. No nut survived to the end of the experiments in 2007 (when seeds were less abundant and rodents were more abundant), whereas 0.3% and 1.5% nuts survived to the end of the experiments in 2008 and 2009 (years with high seed abundance and fewer rodents). Overall, our results suggest that rodents are effective dispersers of *C. indica*, but the dispersal effectiveness is largely dependent on the relative abundances of rodents and available seeds.

Key words: *Castanopsis indica*; Nut; Rodents; Scatter-hoarding; Seed dispersal effectiveness

啮齿动物对印度栲种子扩散的效率

曹林[1,2]　郭聪[1*]

（1 四川大学生命科学学院，生物资源与生态环境教育部重点实验室，成都 610064）

（2 中国科学院动物研究所，农业虫鼠害综合治理研究国家重点实验室，北京 100101）

摘要：从2007年11月到2009年11月，在西双版纳热带雨林中选取三棵母树，在每棵树下每年释放标记印度栲种子200粒（三年共计1 800粒），并追踪其命运。通过调查啮齿动物搬运和分散贮藏印度栲种子的比例，以及调查贮藏种子的微生境、贮藏点大小和扩散距离，分析贮藏种子的存活情况，进而评估啮齿动物对印度栲种子扩散的效率。结果表明，啮齿动物搬运了69.3%的印度栲种子，被搬运的种子中18%被分散贮藏。所有被分散贮藏的种子均被埋于落叶下或埋于土壤表层，并且大部分贮藏点仅含一粒种子。种子的扩散距离从0.5 m到43.8 m，平均距离为7.1 m，扩散距离在年间没有显著差异。2007年（种子密度低，啮齿动物密度高）没有种子能最终存活到实验结束，而2008和2009年（种子密度高，啮齿动物密度低）分别有0.3%和1.5%的种子存活。研究表明，啮齿动物是印度栲有效的种子扩散者，但其扩散效率很大程度上取决于森林中种子的密度和啮齿动物的丰富度。

关键词：印度栲；坚果；啮齿动物；分散贮藏；种子扩散效率

中图分类号：Q958.1　　**文献标识码**：A　　**文章编号**：1000－1050（2011）04－0323－07

1　Introduction

Recruitment of many plants depends on seed dispersal by animals such as frugivores, rodents, and ants (Howe and Smallwood, 1982; Vander Wall, 1990; Herrera, 1995). The effect of dispersal agents on plant recruitment depends upon the seed dispersal effectiveness, which is the contribution made by the dispersers to the plant fitness (Schupp, 1993; Schupp *et al.*, 2010). Seed dispersal effectiveness is usually

Foundation item: The National Natural Science Foundation of China (30930016); the State Basic Research Program (2007CB109102)

Biography: CAO Lin (1980－), Male, PhD, mainly engaged in animal ecology.

Received date: 2011－04－02;　**Accepted date**: 2011－07－28

* Corresponding author, E－mail: guocong@gmail.com

assessed by both quantity and quality of dispersal (Schupp, 1993; Vander Wall, 1993 ; Gomez *et al.*, 2008). The quantity of dispersal is determined by the number of seeds dispersed by the dispersal agents for an individual plant, and the quality of dispersal is determined by the probability that a dispersed seed can survive, germinate and produce a seedling (Schupp, 1993). Seed dispersal effectiveness of frugivorous animals is well understood through the combined efforts of many studies conducted since decades ago (Schupp *et al.*, 2010). However, the seed dispersal effectiveness of scatter-hoarding rodents remains unclear.

The scatter-hoarding rodents are important seed dispersers for many plant species (Vander Wall, 1990; Li and Zhang, 2003; Jansen *et al.*, 2004; Xiao *et al.*, 2004; Roth and Vander Wall, 2005; Xiao *et al.*, 2006), especially for nut species (Vander Wall, 2001). However, in many previous studies, seed removal by small rodents was often argued to be seed predation (Schupp, 1990; Hulme, 2002; Vander Wall *et al.*, 2005a). Although small rodents can remove and cache a large number of seeds, these seeds do not remain in the cache sites for a long time, and most of them are quickly consumed and only a few can survive and germinate (Gomez *et al.*, 2008). Besides, it has been shown that many rodents species prefer to cache seeds in underground burrows (Hollander and Vander Wall, 2004; Lu and Zhang, 2008; Kuhn and Vander Wall, 2009; Chang *et al.*, 2010; Huang *et al.*, 2011) or other larder sites (Somanathan *et al.*, 2007), which are not beneficial to the fitness of plants. All of this evidence indicates that the seed dispersal effectiveness of rodents is relatively low (Gomez *et al.*, 2008). On the other hand, some other studies argued that rodents were effective seed dispersers because after dispersal the few surviving seeds are still important for the recruitment of plant species (Vander Wall, 2001; Vander Wall *et al.*, 2005a; Xiao and Zhang, 2006). Also, rodent dispersal can benefit the plants by taking seeds far away from the parent trees and caching them in suitable micro-sites that are favorable for seed germination (Briggs *et al.*, 2009). However, whether scatter-hoarding rodents are effective seed dispersers remains unclear due to the lack of evidence, because both the rate of dispersal and the survivorship of dispersed seeds are important indices for evaluating the dispersal effectiveness (Schupp, 1993; Schupp *et al.*, 2010).

The objective of this study was to investigate the effectiveness of seed dispersal by small rodents on chinquapin (*Castanopsis indica*) in Xishuangbanna tropical seasonal rain forest. The genus *Castanopsis* contains about 110 species, which are dominant or key species in the tropical and subtropical broad-leaved evergreen forests in East and Southeast Asia (Liu and Zhou, 2006). Seed dispersal of some other genera (e.g. *Quercus* and *Fagus*) in Fagaceae by scatter-hoarding rodents is well understood (Vander Wall, 2001); however, the dispersal ecology of *Castanopsis* is still poorly known. In this study we investigate the quantity and quality of seed dispersal in order to assess the dispersal effectiveness. We assess the quantity of dispersal by using (1) the proportion of experimental nuts moved away from the seed stations. For the quality of dispersal we consider (2) the proportions of cached nuts buried beneath leaf litter or in soil, (3) the number of nuts per cache (cache size), (4) the distance of nuts transported, and finally (5) the proportion of nuts surviving after removal by rodents.

2 Materials and methods

2.1 Study site

This study was conducted in a tropical seasonal rain forest of the Menglun Nature Reserve, Xishuangbanna, Yunnan Province, China, a region that has a typical tropical monsoon climate characterized by distinct wet and dry seasons. The average annual rainfall is approximately 1 500 mm, 80% of which is during the wet season (May – October) and 20% during the dry season (November – April). The average annual temperature is 21.7℃ (Cao and Zhang, 1997). The study site is located in a wet valley, near a permanent plot of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (21°50′N, 101°12′E, elevation 780 m). The forest is dominated by *Pometia tomentosa* and *Terminalia myriocarpa* with an average canopy height of 30 m (Zhang and Cao, 1995).

Castanopsis indica is widely distributed in south Asia, and is commonly seen in Xishuangbanna tropical seasonal rain forests, where a few nut-bearing tree species occur. The nuts of *C. indica* are protected by dense spines. Burs contain only one seed, and mature from late September to December. The mean fresh nut mass is 1.3 ± 0.2 g (mean ± SD), varying from 0.2 g to 3.0 g. The nuts germinate very quickly after falling to the ground, usually within 1 – 2 weeks under favorable conditions. Different from many other species of *Castanopsis* (e.g. *C. echidnocarpa* and *C. hys-*

trix) in the study site, *C. indica* has not shown marked mast seeding (Cao Lin personal observation). The crops of *C. indica* nuts were very low from 2007 to 2009. However, *Lithocarpus magneinii* and *C. echinocarpa* showed marked mast seeding in 2008 and 2009, respectively, in the study site. Many nuts of *L. magneinii* and *C. echinocarpa* fell to the ground after ripening, and remained for a long time under the parent trees (Cao, 2009; Cao Lin personal observation).

Small rodents are important seed predators and dispersers of *Castanopsis* (Roth and Vander Wall, 2005; Xiao *et al.*, 2005a). In the study site, three commonly seen rodent species (*Niviventer confucianus*, *N. fulvescens* and *Maxomys surifer*) scatter and larder-hoard seeds, and one species (*Rattus flavipectus*) larder-hoards seeds (Cao *et al.*, 2011). In addition, three species of tree squirrel (*Dremomys rufigenis*, *Callosciurus erythraeus* and *Tamiops swinhoei*) also are potential seed dispersers.

2.2　Seed releasing experiments

Experiments were conducted in mid-November every year from 2007 to 2009. One thousand and eight hundred round nuts were used for seed releasing experiments. In mid-November of each year, 600 tagged nuts were placed under three focal trees (200 nuts for each tree), which were spaced > 30 m along a transect. For each focal tree, we constructed 4 seed stations within 2 m radius from the tree trunk, and 50 tagged nuts were placed on the ground surface at each station. Each nut was marked by attaching to a small coded plastic tag using a thin 16 cm long steel thread (Zhang and Wang, 2001; Xiao *et al.*, 2006). After rodents buried the tagged nuts beneath leaf litter or in soil, the tags were exposed on the surface and can easily be relocated. This tagging method has insignificant effect on the patterns of seed dispersal by rodents (Xiao *et al.*, 2006). The fate of the released nuts was surveyed 1, 4, 7, 14, 28 and 56 days after placement. During each visit, we searched the area around each focal tree (search area diameter: 30 – 80 m) to retrieve the tagged nuts and to record their fate. Nuts at seed stations were categorized as remaining, eaten, and removed, whereas tagged nuts removed from the seed stations were categorized as cached (primary cache, buried beneath leaf litter or in the soil), eaten, or missing. During our survey, we also found that some nuts hoarded in underground burrows or in tree holes, where nuts may finally be eaten, and this was not beneficial to the fitness of parent plants. These nuts were thus categorized as consumed (eaten). For dispersed nuts, we also recorded the micro-sites and distance from the focal trees. Cached nuts were marked using a numbered bamboo stick 20 cm away. During subsequent visits, we also checked the cached nuts found in previous visits until they were recovered (eaten or removed from cache sites) by animals. If a marked cache was removed, the area around the cache was extensively searched in a radius of 10 – 20 m. When nuts in primary or higher order caches (e.g. secondary caches, caches after primary caching) were removed and found in other cache sites, we also recorded their fate, micro-sites and distances from focal trees.

2.3　Trapping of small rodents

We monitored rodent populations in September and December from 2007 to 2009. 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) baited with fresh peanuts (Chang *et al.*, 2009). Trapping was conducted for three consecutive days per season (150 trap days). Captured rodents were identified, weighed and released immediately *in situ*.

2.4　Statistics and analysis

SPSS for Windows (13.0) was used for data analyses. Chi-square and Fisher's exact test were used for testing differences for the trap success of rodents. The Cox regression was used for comparing the differences of mean lifetime (mean ± SE days, $n = 600$ nuts per year) of tagged nuts under focal trees among three years, and survival time (mean ± SE days) of nuts in the cached sites among three years. Logistic regression models were used to test the differences of the proportion of nut removal (% mean ± SD, $n = 3$ trees per year) under focal trees and the proportion of nuts cached (% mean ± SD, $n = 3$ trees per year) after removal from focal trees among three years. One-way ANOVA was used to test differences in dispersal distance (mean ± SD m, log-transformed to meet normal distribution) of cached nuts among three years.

3　Results

3.1　Population abundance of small rodents

During the three study periods, 38 rodent individuals of five species (*N. confucianus*, *N. fulvescens*, *M. surifer*, *R. flavipectus* and *D. rufigenis*) were captured. The dominant species was *N. confucianus* ($n = 31$, 81% of total) and *M. surifer* ($n = 4$, 10.5% of total). Only one individual each of the other 3 species was captured. This result was consistent with a previous study (Wu *et al.*, 1996). Trap success rate was 8.7% in 2007 (n = 26), significantly higher than in 2008 (0.3%, n = 1; Fisher's exact test: df = 1, P < 0.001) and 2009 (3.7% n = 11; chi-square test: χ^2 = 6.481, df = 1, P = 0.011).

3.2 Nut removal and caching

Small rodents harvested (ate or removed) all the tagged nuts within one day after nut placement in 2007, and within 28 days in 2008 and 2009 (Fig. 1). Nut lifetime at the seed stations was significantly different among the three years (Cox regression, Wald = 583.414, df = 2, P < 0.001). The mean nut lifetime at seed stations in 2008 (16.9 ± 0.3 days) and 2009 (6 ± 0.1 days) were 16.9 and 6 times longer, respectively, than in 2007 (1 day).

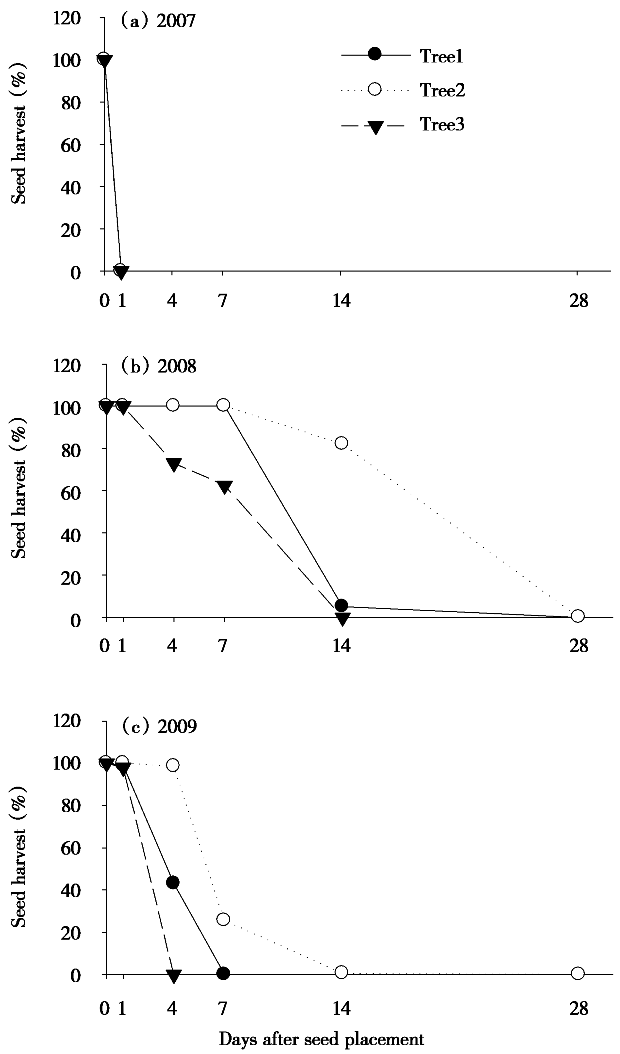

Fig. 1 Seed harvest of *Castanopsis indica* by small rodents after nut placement under three focal trees in 2007 (all nuts were harvested within one day for all 3 trees), 2008 and 2009.

Rodents removed 69.3% (from 56 to 91.2%) of the tagged nuts and consumed the rest under focal trees in all three years (Fig. 2). The proportion of nuts that were moved away from focal trees was significantly different among three years as shown by logistic regression (χ^2 = 168.182, df = 2, P < 0.001). The proportion of nuts removed in 2007 was 91.2 ± 3.7%, which was significantly higher than that in 2008 (56.0 ± 7.5%, n = 3 trees, χ^2 = 159.527, df = 1, P < 0.001) and in 2009 (60.7 ± 18.5%, χ^2 = 130.531, df = 1, P < 0.001) (Fig. 2). Of these removed nuts, 59.7% (from 48.9 to 64.9%) were consumed immediately, 18% (from 4.9 to 42%) were found cached (primary cache), and the rest were missing (Fig. 2). We found that the proportion of cached nuts was significantly different among three years (χ^2 = 214.424, df = 2, P < 0.001). The proportion of cached nuts in 2009 (25.5 ± 5.7% of the tagged nuts) was 5.7 and 3.4 times higher than in 2007 (4.5 ± 5.6%) and 2008 (7.5 ± 5.2%) respectively (Fig. 2). Most cached nuts (primary cache) were quickly recovered by rodents. 70.7% (from 57.8 to 81.5%) of them were consumed immediately, and 7.1% (n = 16) were moved into new cache sites (secondary cache) nearby (Fig. 2). No nuts were found in secondary caches in 2007, while 2 nuts and 14 nuts were found in 2008 and 2009 respectively (Fig. 2). In 2009, we also found 3 nuts in tertiary caches. All of the cached nuts were buried beneath leaf litter or in the soil, where the nuts possibly survived and produced new recruits. All cached nuts were deposited under shrubs or in grasses. For these caches, most of them (n = 180) contained only one single nut for each cache, and a few (n = 14) contained 2 – 3 nuts. Two large were found, one in 2007 (contained 19 nuts) and one in 2009 (contained 13 nuts).

3.3 Dispersal distance

We relocated 225 cached nuts in three years. The dispersal distances of primary caches ranged from 0.5 to 47.5 m, but most were < 10 m. The primary dispersal distance of cached nuts varied little among three years ($F_{2,224}$, n = 0.886, P = 0.414). The dispersal distance of primary caches in 2007 was 8.1 ± 8.6 m (n = 27 nuts), slightly farther than in 2008 (6.7 ± 5.8 m, n = 45 nuts) and 2009 (7.1 ± 6.1 m, n = 153 nuts).

3.4 Nut survival

Most cached nuts did not survive for long in cache sites, and only a very few nuts survived to the end of the experiment. The survival time of nuts in the

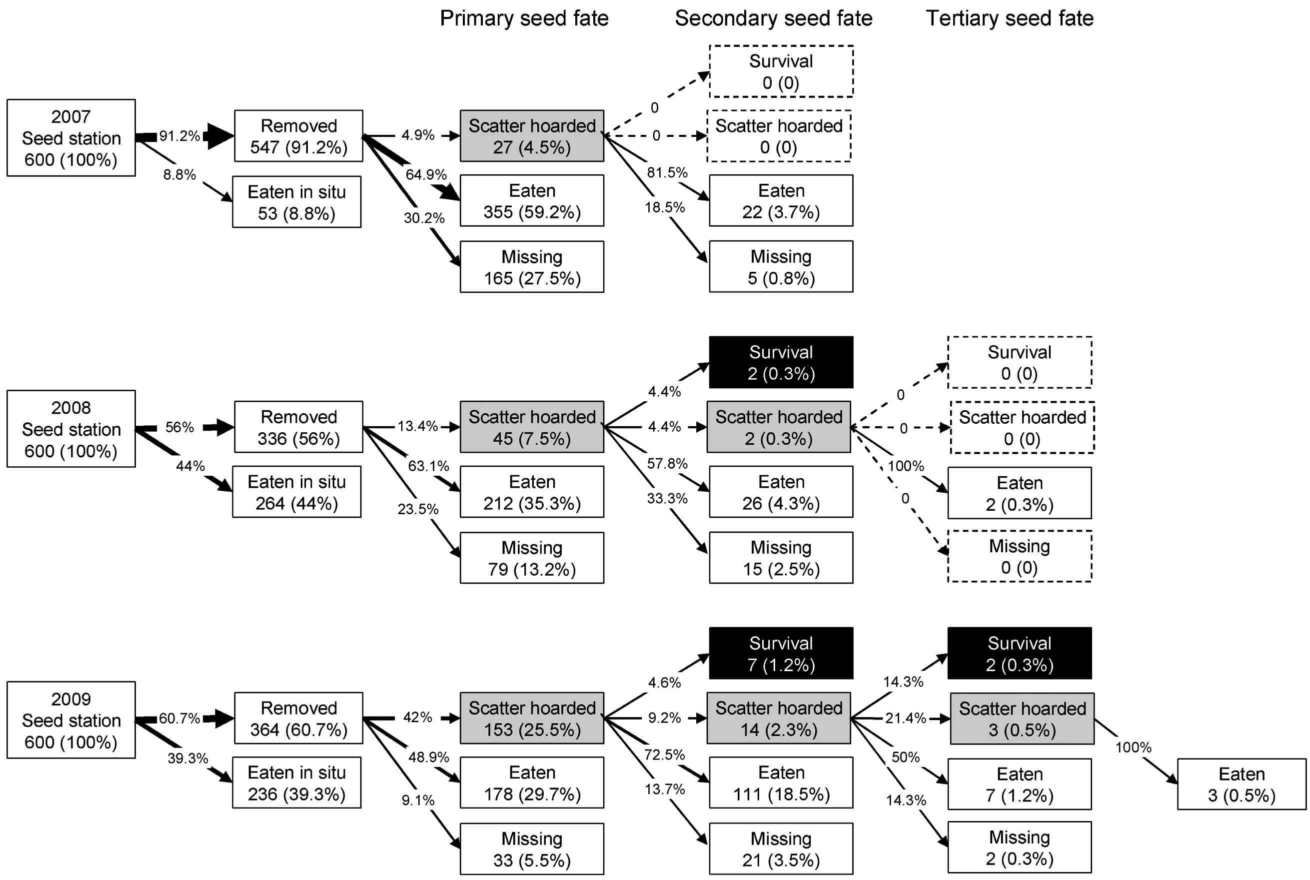

Fig. 2　Seed fate pathways of the tagged nuts of *Castanopsis indica* after placement under focal trees from 2007 to 2009

cached sites was significantly different among the three years (Wald = 583.414, $df = 2$, $P < 0.001$). The mean survival time of cached nuts in 2008 and 2009 was 22.4 ± 2.1 days (n = 45 nuts) and 23.4 ± 1.8 days (n = 153 nuts), respectively, 5.9 and 6.2 times higher than in 2007 (3.8 ± 0.3 days, n = 27 nuts). There was considerable annual variation for nut survival. No nut survived to the end of the experiment in 2007, whereas 2 (0.3 %) and 9 (1.5%) nuts survived to the end of the experiment in 2008 and 2009, respectively (Fig. 2). Nine of the surviving nuts were from the primary cache sites, and two from the secondary caches. We also found that 6 of the surviving nuts germinated at the end of the experiment.

4 Discussion

Through our experiments, we found that rodents handled all of the tagged nuts within 4 weeks and dispersed most of them. The results suggest that the quantity of seed dispersal to the *C. indica* performed by rodents is high. This high seed dispersal is consistent with that of many other cases of nut-bearing trees (Schupp, 1993; Hollander and Vander Wall, 2004; Roth and Vander Wall, 2005; Xiao and Zhang, 2006; Gomez *et al.*, 2008). After removal from focal trees, most dispersed nuts were consumed immediately following dispersal. However, we also found 12.5% (4.5% to 25.5% over three years) of the tagged nuts were cached beneath leaf litter or in the soil. The proportion of cached nuts was at a moderate level (Vander Wall, 1993; Roth and Vander Wall, 2005; Xiao and Zhang, 2006; Gomez *et al.*, 2008). All of the cached nuts were buried beneath leaf litter or in the soil, and most caches contained only one single nut. These caching characteristics will favor seed germination and seedling establishment, and will further favor the surviving of the seedling (Hollander and Vander Wall, 2004; Roth and Vander Wall, 2005; Briggs *et al.*, 2009). We found that cached nuts germinated very quickly, and 6 of the surviving nuts germinated by the end of the experiment. These results indicate that seed dispersal by rodents also benefits the recruitment of the plants, when compared with non seed-predator dispersers which deposit seeds in clusters on the ground surface (Vander Wall *et al.*, 2005b).

The definition of seed dispersal effectiveness implies not only the dispersal of seeds but also the survivorship of dispersed seeds (Schupp, 1993). In our study, we found a large number of nuts cached after removal; most cached nuts were quickly recovered and consumed by rodents. However, we found that 0.61% of the tagged nuts survived to the end of the experiments across the three years. But nut survival varied greatly among three years. Our results show that the high proportion of nut removal (in 2007) does not necessarily equal high proportion of scatter-hoarding or even nut survival given that the quality of seed dispersal is determined by multiple factors (Schupp *et al.*, 2010). High seed abundance or low rodent population sizes (in 2008 and 2009) could potentially promote scatter-hoarding and survival of dispersed seeds (Jansen *et al.*, 2004; Li and Zhang, 2007), but at the cost of low seed removal. In our study site, seed abundance was very low and the rodent population was relatively high in 2007 compared with the other two years. This may explain why few nuts were found cached and no nut survived in 2007, while 0.3% and 1.5% nuts survived in 2008 and 2009. These results indicate that the seed dispersal effectiveness performed by rodents varies between years.

Besides the survivorship of seeds, the quality of seed dispersal is also dependent on the distance the seeds are transported and on the micro-sites where seeds are deposited. Long distance dispersal is very important because it enables a plant to colonize new habitat patches, and could also reduce density-dependent mortality as predicted by the Janzen-Connell model (Janzen, 1970; Connell, 1971). Rodents did not transport the nuts of *C. indica* for long distances (mean dispersal distance was only 7.1 ± 6.4 m), which is similar to other nut-bearing trees with seeds dispersed by rodents (Vander Wall, 2002; Xiao *et al.*, 2004; Xiao *et al.*, 2005b; Moore *et al.*, 2007; Gomez *et al.*, 2008). Though most cached nuts were found within 10 m from focal trees, a few were transported more than 30 m away, suggesting that long distance dispersal of *C. indica* seeds by small rodents is possible.

I conc usio , we f und r dent disp rsed ost tagge nuts f *C. indic* an cach d man of th m, i dica ing s ed di pers l in t is ca e is o high uant-t . Als , rod nts d sper ed nu s far rom f cal t ees, and c ched hem i suit ble m cro-ites hat w re fa vo able or re ruit ent. A ew nu s sur ived o the nd of t e exp rime ts an germ nate . How ver, ut su -v vors ip va ied g eatl amon the t ree y ars. ur re su ts su gest hat r dent are e fect ve se d dis erse s of *C. in ica*, but he di pers l eff ctiv ness s lar ely depen ent o the r lati e abu danc of ro ents nd a-vai able eeds n the ores.

Acknowledgements: This work was supported by the open fund from the CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. We are grateful to the Xishuangbanna Station of Tropical Rainforest Ecosystem Studies for the kind support to our field work.

References:

Briggs J S, Vander Wall S B, Jenkins S H. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology*, **90**: 675-687.

Cao L. 2009. Effects of mast seeding on seed predation, dispersal and caching by small rodents in Xishuangbanna tropical forest. PhD Thesis, Sichuan University, Chengdu.

Cao L, Xiao Z S, Wang Z Y, Guo C, Chen J, Zhang Z B. 2011. High regeneration capacity helps tropical seeds to counter rodent predation. *Oecologia*, DOI 10.1007/s00442-011-1908-1, in press.

Cao M, Zhang J H. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodivers Conserv*, **6**: 995-1006.

Chang G, Xiao Z S, Zhang Z B. 2009. Hoarding decisions by Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*): The responses to seed size and germination schedule in acorns. *Behav Process*, **82**: 7-11.

Chang G, Xiao Z S, Zhang Z B. 2010. Effects of burrow condition and seed handling time on hoarding strategies of Edward's long-tailed rat (*Leopoldamys edwardsi*). *Behav Process*, **85**: 163-166.

Connell J H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer P J, Gradwell G eds. Dynamics of Populations. PUDOC, 298-312.

Gomez J M, Puerta-Pinero C, Schupp E W. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia*, **155**: 529-537.

Herrera C M. 1995. Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, evolutionary, and historical determinants. *Annu Rev Ecol Syst*, **26**: 705-727.

Hollander J L, Vander Wall S B. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). *Oecologia*, **138**: 57-65.

Howe H F, Smallwood J. 1982. Ecology of seed dispersal. *Annu Rev Ecol Syst*, **13**: 201-228.

Huang Z Y, Wang Y, Zhang H M, Wu F Q, Zhang Z B. 2011. Behavioural responses of sympatric rodents to complete pilferage. *Anim Behav*, **81**: 831-836.

Hulme P E. 2002. Seed-eaters: seed dispersal, destruction and demography. In: Levey D J, Silva W R, Galetti M eds. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International, Wallingford, UK, 257-273.

Jansen P A, Bongers F, Hemerik L. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol*

Monogr, **74**: 569 – 589.

Janzen D H. 1970. Herbivores and the number of tree species in Tropical forests. *Am Nat*, **104**: 501 – 528.

Kuhn K M, Vander Wall S B. 2009. Formation and contents of yellow-pine chipmunk (*Tamias amoenus*) winter larders. *West N Am Naturalist*, **69**: 309 – 318.

Li H J, Zhang Z B. 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). *Forest Ecol Manag*, **176**: 387 – 396.

Li H J, Zhang Z B. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecol Manag*, **242**: 511 – 517.

Liu M Q, Zhou Z K. 2006. Modern and geological distribution of *Castanopsis* (Fagaceae). *Acta Botanica Yunnanica Sinica*, **28**: 223 – 235.

Lu J Q, Zhang Z B. 2008. Differentiation in seed hoarding among three sympatric rodent species in a warm temperate forest. *Integrative Zoology*, **3**: 134 – 142.

Moore J E, McEuen A B, Swihart R K, Contreras T A, Steele M A. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology*, **88**: 2529 – 2540.

Roth J K, Vander Wall S B. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatterhoarding rodents. *Ecology*, **86**: 2428 – 2439.

Schupp E W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a Neotropical tree. *Ecology*, **71**: 504 – 515.

Schupp E W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, **108**: 15 – 29.

Schupp E W, Jordano P, Gomez J M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytol*, **188**: 333 – 353.

Somanathan H, Mali S, Borges R M. 2007. Arboreal larder-hoarding in the tropical Indian giant squirrel *Ratufa indica*. *Ecoscience*, **14**: 165 – 169.

Vander Wall S B. 1990. Food hoarding in animals. Chicago: University of Chicago Press, 1 – 445.

Vander Wall S B. 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia*, **96**: 246 – 252.

Vander Wall S B. 2001. The evolutionary ecology of nut dispersal. *The Botanical Review*, **67**: 74 – 117.

Vander Wall S B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology*, **83**: 3508 – 3516.

Vander Wall S B, Kuhn K M, Beck M J. 2005a. Seed removal, seed predation, and secondary dispersal. *Ecology*, **86**: 801 – 806.

Vander Wall S B, Kuhn K M, Gworek J R. 2005b. Two-phase seed dispersal: linking the effects of frugivorous birds and seed-caching rodents. *Oecologia*, **145**: 282 – 287.

Wu D L, Luo J, Fox B J. 1996. A comparison of ground-dwelling small mammal communities in primary and secondary tropical rainforests in China. *J Trop Ecol*, **12**: 215 – 230.

Xiao Z S, Jansen P A, Zhang Z B. 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecol Manag*, **223**: 18 – 23.

Xiao Z S, Zhang Z B. 2006. Nut predation and dispersal of Harland Tanoak *Lithocarpus harlandii* by scatter-hoarding rodents. *Acta Oecol*, **29**: 205 – 213.

Xiao Z S, Zhang Z B, Wang Y S. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *Forest Ecol Manag*, **195**: 141 – 150.

Xiao Z S, Zhang Z B, Wang Y S. 2005a. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii* (Fagaceae). *Plant Ecol*, **177**: 249 – 257.

Xiao Z S, Zhang Z B, Wang Y S. 2005b. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecol*, **28**: 221 – 229.

Zhang J H, Cao M. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biol Conserv*, **73**: 229 – 238.

Zhang Z B, Wang F S. 2001. Effect of rodents on seed dispersal and survival of wild apricot *Prunus armeniaca*. *Acta Ecology Sinica*, **21**: 839 – 845.