

ORIGINAL ARTICLE

Scatter-hoarding rodents as secondary seed dispersers of a frugivore-dispersed tree *Scleropyrum wallichianum* in a defaunated Xishuangbanna tropical forest, China

Lin CAO,^{1,2,3} Zhishu XIAO,² Cong GUO,¹ Jin CHEN³

¹Key Laboratory of Bio-resources and Eco-environment, Ministry of Education, College of Life Science, Sichuan University, Chengdu, China, ²State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing, China and ³Chinese Academy of Sciences, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Abstract

Local extinction or population decline of large frugivorous vertebrates as primary seed dispersers, caused by human disturbance and habitat change, might lead to dispersal limitation of many large-seeded fruit trees. However, it is not known whether or not scatter-hoarding rodents as secondary seed dispersers can help maintain natural regeneration (e.g. seed dispersal) of these frugivore-dispersed trees in the face of the functional reduction or loss of primary seed dispersers. In the present study, we investigated how scatter-hoarding rodents affect the fate of tagged seeds of a large-seeded fruit tree (*Scleropyrum wallichianum* Arnott, 1838, Santalaceae) from seed fall to seedling establishment in a heavily defaunated tropical forest in the Xishuangbanna region of Yunnan Province, in southwest China, in 2007 and 2008. Our results show that: (i) rodents removed nearly all *S. wallichianum* seeds in both years; (ii) a large proportion (2007, 75%; 2008, 67.5%) of the tagged seeds were cached individually in the surface soil or under leaf litters; (iii) dispersal distance of primary caches was further in 2007 (19.6 ± 14.6 m) than that in 2008 (14.1 ± 11.6 m), and distance increased as rodents recovered and moved seeds from primary caches into subsequent caching sites; and (iv) part of the cached seeds (2007, 3.2%; 2008, 2%) survived to the seedling stage each year. Our study suggests that by taking roles of both primary and secondary seed dispersers, scatter-hoarding rodents can play a significant role in maintaining seedling establishment of *S. wallichianum*, and are able to at least partly compensate for the loss of large frugivorous vertebrates in seed dispersal.

Key words: frugivorous vertebrate, scatter-hoarding rodents, *Scleropyrum wallichianum*, seed dispersal, seedling recruitment.

Correspondence: Cong Guo, Key Laboratory of Bio-resources and Eco-environment, Ministry of Education, College of Life Science, Sichuan University, Chengdu 610064, China.
Email: guocong@gmail.com

Jin Chen, CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China.
Email: cj@xtbg.org.cn

INTRODUCTION

Seed dispersal by vertebrates is a crucial process in plant regeneration (Herrera 1995). However, this process is under serious threat. Many seed dispersers, especially large vertebrates, are experiencing drastic declines in population (some to the point of extinction) at local, regional and even global scales, caused by human disturbances, such as hunting and habitat change (Corlett 1998; Peres

2000; Alroy 2001; Lyons *et al.* 2004; Burney & Flannery 2005; Guimaraes *et al.* 2008). Large vertebrates often play essential roles in seed dispersal and natural regeneration of large-seeded fruit trees (Fragoso 1997; Guimaraes *et al.* 2008). Local extinction or population decline of these large frugivorous vertebrates might lead to dispersal limitation of large-seeded fruit trees (Wright *et al.* 2000; Guimaraes *et al.* 2008; Holbrook & Loiselle 2009; Corlett 2011); this is especially true in tropical forests where many plant species rely heavily on vertebrates for seed dispersal (Corlett 1998, 2011).

For many fruiting species, seed dispersal is a complex, multi-step process involving several dispersal agents/guilds, who offer different benefits to plants across different dispersal stages (Vander Wall & Longland 2004). For example, many frugivorous vertebrates as primary dispersal agents often consume fruit pulp and disperse seeds by defecation or regurgitation, but the defecated or regurgitated seeds are also harvested and dispersed by scatter-hoarding rodents as secondary seed dispersers (Vander Wall & Longland 2004). Growing evidence shows that scatter-hoarding rodents act as primary dispersal agents for many large-seeded plants, such as nut-bearing species (e.g. Vander Wall 2001; Zhang *et al.* 2005). In addition, scatter-hoarding rodents might also play an important role in secondary seed dispersal of fallen fruits (e.g. Brewer & Rejmanek 1999; Wright 2003). However, it is largely unknown whether scatter-hoarding rodents as secondary seed dispersers can help maintain natural regeneration of large-seeded fruit trees in the face of the functional reduction or losses of their primary seed dispersers.

Some recent studies suggest that defaunation (e.g. loss of large frugivorous vertebrates in particular) might have a negative impact on seedling recruitment of many fruiting species producing large seeds (Cardoso da Silva & Tabarelli 2000; Wright 2003; Guimaraes *et al.* 2008; Holbrook & Loiselle 2009). However, compensation of seed dispersal by other sympatric animals might reduce such negative effects due to disappearance of primary seed dispersers (Brewer & Rejmanek 1999; Wright *et al.* 2000; Wright 2003). In general, scatter-hoarding rodents might be less affected than large frugivorous vertebrates because the former might experience lower hunting pressures and/or these rodents are less sensitive to habitat changes (Wright 2003; Dirzo *et al.* 2007). Therefore, secondary seed dispersal by scatter-hoarding rodents might be important for the persistence of large-seeded fruit species after extinction or decline of their primary seed dispersers (Tabarelli & Peres 2002; Guimaraes *et al.* 2008). We contend that scatter-hoarding rodents might compensate for seed dispersal of large-seeded

trees to some extent after local extinction or population decline of large vertebrate frugivores (Wright 2003). However, few studies have been conducted to investigate the effects of scatter-hoarding rodents on seed dispersal and natural regeneration of large-seeded fruit species in defaunated areas (e.g. Brewer & Rejmanek 1999; Guimaraes *et al.* 2008).

In the present study, we investigate how scatter-hoarding rodents affect the fate of tagged seeds of a large-seeded fruit tree (*Scleropyrum wallichianum*, Santalaceae) from seed fall to seedling establishment in a heavily defaunated tropical forest in the Xishuangbanna region of Yunnan Province, south-west China, in 2007 and 2008. The fruits of *S. wallichianum* are very large (mean 40.9 g) and rich in nutrients, and should be dispersed by large frugivorous vertebrates (e.g. primates and deer) in their habitats (but see Guimaraes *et al.* 2008). As a result of extensive human disturbances to tropical forest in the Xishuangbanna region in recent decades, populations of large vertebrates have declined, leading, in some cases, to extinction. According to our recent survey, piles of *S. wallichianum* fruits are found rotten under parent trees, but some seedlings are found established at sites far from parent trees. This suggests that other seed/fruit-eating animals (e.g. scatter-hoarding rodents, L. Cao, pers. observ.) might take over the role of seed dispersal by large frugivorous vertebrates. We found that several rodent species scatter-hoarded tree seeds such as *Pittosporopsis kerrii* (Craib, 1911), *Garcinia cowa* (Roxburgh, 1832), *Garcinia xanthochymus* (Hooker f. ex T. Anderson, 1874), *Castanopsis echidnocarpa* (A. DC., 1863), *Castanopsis calathiformis* (Rehder et Wilson, 1916), *Lithocarpus truncatus* (Rehder et Wilson, 1916) and *Lithocarpus leucostachyus* (A. Camus, 1934) and, therefore, they are important for natural regeneration of these large-seeded species (e.g. Cao *et al.* 2011; Cao *et al.*, unpubl. data). Therefore, we expect that scatter-hoarding rodents, as secondary seed dispersers, are capable of contributing greatly to successful seed dispersal and seedling establishment of *S. wallichianum* in the face of the functional reduction or loss of primary seed dispersers in the Xishuangbanna tropical forests.

MATERIALS AND METHODS

Study sites

This study was conducted in a tropical montane evergreen broad-leaf forest of the Menglun Nature Reserve (21°50'N, 101°12'E, elevation 780 m) in the Xishuangbanna region of Yunnan Province, south-west China. The average annual rainfall is approximately 1500 mm, with 80% in the wet season (May–October) and 20% in the dry season

(November–April) (Cao & Zhang 1997). The average annual temperature is 22 °C. The forest is dominated by *C. echidnocarpa*, *Aporosa yunnanensis*, *Olea rosea*, *L. truncates* and *Schima wallichii* (Zhang & Cao 1995).

Scleropyrum wallichianum is a small tree (approximately 10 m in height) that is widely distributed in south and south-east Asia (including south China), and is commonly found in the Xishuangbanna tropical forests (Wu 1987). *S. wallichianum* produces large rounded fruits with only 1 seed per fruit. The fruit crop was 216 ± 138 fruits per tree (mean \pm SD, $n = 5$, range from 16 to 366 fruits) in 2008. The fruit mass is 40.9 ± 7.0 g, fruit length is 5.9 ± 0.3 cm, fruit diameter is 3.9 ± 0.4 cm; seed mass is 4.7 ± 0.7 g, seed length is 2.2 ± 0.1 cm, seed diameter is 1.8 ± 0.1 cm and the thickness of the endocarp is 1.9 ± 0.3 mm ($n = 30$). Seed endosperms have high fat content (approximately 66.8%). *S. wallichianum* fruits become mature from August to September. According to the published literature and local residents (pers. survey), there are some large mammals that lived in the study site about thirty years ago (e.g. non-human primates, *Nycticebus coucang bengalensis* and *Macaca mulatta*, deer, *Muntiacus muntjak vaginalis*, and civets, *Paguma larvata*) (see Xu & Jiang 1987). These animals have been observed to consume fruits from *S. wallichianum* and other fruiting plants by local people at the study site (interviews with local residents conducted by L. Cao). Obviously, these mammals might act as important primary dispersal agents for *S. wallichianum* and other fruiting plants in the Xishuangbanna tropical forests and/or in tropical Asia (Corlett 1998). However, these large mammals are rarely seen at the study site due to extensive human disturbances, such as hunting and deforestation. In our recent survey, seed-eating rodents, including tree squirrels (e.g. *Dremomys rufigenis* (Blanford, 1878) and *Callosciurus erythraeus* (Pallas, 1779)) and Muridae species (e.g. *Niviventer confucianus* (Milne-Edwards, 1871), *Niviventer fulvescens* (Gray, 1847) and *Maxomys surifer* (Miller, 1900)) were observed eating and removing the *S. wallichianum* seeds. In addition, we also found that several rodent species (e.g. *N. confucianus*, *N. fulvescens* and *M. surifer*) scatter-hoarded seeds from *P. kerrii* and other large-seeded species at the study site (Cao *et al.* 2011; L. Cao *et al.*, unpubl. data; see also Liu *et al.* 2002).

Experimental design

We tracked the fate of individual *S. wallichianum* seeds at the study site from August (rainy season) to the following spring, for 2 years (2007 and 2008). After *S. wallichianum* fruit ripened, we collected enough fruit from the ground under 3 parent trees each year, and removed the fresh pulp

to collect seeds for seed dispersal experiments. Seeds were marked by attaching a small coded plastic tag to each seed through a 16 cm thin steel thread (Xiao *et al.* 2006). When rodents buried the tagged seeds beneath leaf litters or in the soil, the tags were exposed on the surface, making them easy to relocate. This tagging method has a negligible effect on patterns of seed dispersal by rodents (Xiao *et al.* 2006).

In September 2007 and 2008, 200 tagged seeds were placed under each of the 3 same fruiting trees (600 seeds in total), and these focal trees were spaced more than 50 m apart from each other. For each focal tree, we established 4 seed stations in 4 directions within 2 m of the tree's trunk, and placed 50 tagged seeds on the ground at each station. The fate of the tagged seeds were surveyed at weeks 2, 4, 8, 12 and 16 of the current year, and then in March, July, September and December of the following year. During each survey, we searched the area around each focal tree (diameter: 30–80 m) to retrieve the tagged seeds and record seed fate. Seeds under the focal tree were categorized as remaining, eaten and removed, and those removed from seed station were categorized as cached (intact seeds buried in the surface soil or beneath leaf litters), eaten (consumed by rodents leaving only tags and seed fragments), or missing (fate unknown). For cached seeds, we also recorded the micro-sites, cache size (number of seeds in a cache) and distances from the focal trees. Cached seeds were marked using a numbered bamboo stick. At subsequent visits, we checked the cached seeds located in previous visits until they were recovered (eaten or removed) by animals. If a marked cache was removed, the area around the cache was extensively searched. When seeds in primary caches or higher-order caches (e.g. secondary caches, hoarded after primary caching; tertiary caches, hoarded after secondary caching) were removed and found in other caching sites, we also recorded seed fate, micro-sites and distances from the focal trees. We surveyed all previously cached sites to determine whether some of the cached seeds had established seedlings in March, July, September and December of the following 2–3 years. We also monitored pre-dispersal and post-dispersal seed infestation by insects and fungi.

Statistics and analysis

SPSS for Windows (13.0) was used for data analyses. The Cox regression was used for comparing the differences of the mean lifetime of tagged seeds between the 2 years. Logical regression models were used to test the differences in the proportion of seeds found in primary, secondary and tertiary caches between the 2 years and among trees. Logical regression models were also used

for testing differences in the probabilities of seedling establishment. Independent samples *t*-test was used to test the difference in dispersal distances (log-transformed to meet assumption of normality) between the 2 years. Repeated-measures analysis of variance was used to test the difference in dispersal distances from 14 seeds at 3 caching stages, because they were moved up to 3 times (i.e. from primary to tertiary caches).

RESULTS

Rodents harvested nearly all the tagged seeds each year, at faster rates in 2007 than in 2008 (Wald = 583.414, $df = 1$, $P < 0.001$) (Fig. 1). The mean lifetime of the tagged seeds in 2007 (mean \pm SE, 2.2 ± 0.1 weeks) was much shorter than in 2008 (7.3 ± 0.2 weeks). No seeds were infested by insects or fungi at seed stations. Rodents *in situ* consumed 14 seeds (2007, $n = 1$; 2008, $n = 13$) and removed all the other seeds (mean \pm SD, 2007, $99.8 \pm 0.2\%$; 2008, $97.8 \pm 1.5\%$) during the 2 years (Fig. 2a).

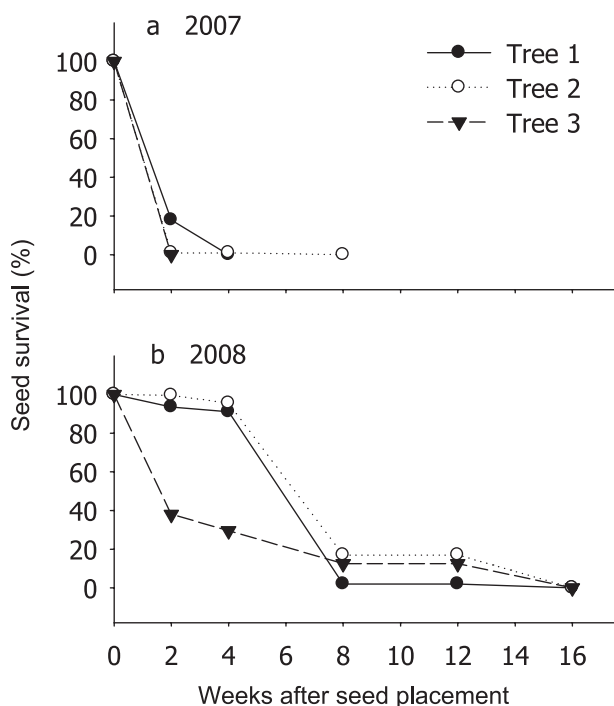


Figure 1 Survival curve (proportion) of tagged seeds of *Scleropyrum wallichianum* after placement under 3 focal trees in (a) 2007 and (b) 2008.

We relocated most (2007, 82.3%; 2008, 88%) of the tagged seeds after they were removed from the focal trees. More removed seeds were hoarded in primary caching sites in 2007 ($75 \pm 12.3\%$) than in 2008 ($67.5 \pm 8.8\%$) ($Z = 5.502$, $P = 0.019$) (Fig. 2b), and 1.2% of them were larder-hoarded in underground burrows and tree holes and finally eaten by rodents (this data was not included in the analysis). The proportion of hoarded seeds in primary caches was not significantly different among the 3 focal trees ($Z = 1.766$, $P = 0.414$). For each year, the seeds in primary caches were quickly recovered, and some of them were moved into new sites as secondary caches (Fig. 2c). Some seeds in secondary caches were also recovered and then moved into tertiary caches (Fig. 2d). The proportion of seeds in secondary caches was significantly higher in 2007 ($24.8 \pm 9.2\%$) than in 2008 ($9.3 \pm 2.9\%$) ($Z = 43.717$, $P < 0.001$), but that proportion in tertiary caches was a little higher in 2007 ($2.0 \pm 1.8\%$) than in 2008 ($0.3 \pm 0.6\%$) ($Z = 1.51$, $P = 0.219$).

Most of the cached seeds were buried beneath leaf litters during the 2 years of observation (98.5% for primary caches, 99% for secondary caches and 85.7% for tertiary caches), and the rest were buried in the surface soil. In addition, nearly all caches contained only a single seed for each cache (primary cache, $n = 841$; secondary cache, $n = 202$; tertiary cache, $n = 14$) and very few caches contained 2 seeds (primary cache, $n = 7$; secondary cache, $n = 1$).

Dispersal distance for primary caches ranged from 0.8 to 88 m, while that for secondary and tertiary caches ranged from 3.9 to 121 m and from 26.2 to 75 m, respectively. The dispersal distance of primary caches in 2007 was 19.6 ± 14.6 m (mean \pm SD), significantly farther than that in 2008 (14.1 ± 11.6 m) ($t = 6.131$, $df = 853$, $P < 0.001$) (Fig. 3). The dispersal distances of secondary caches were similar in 2007 (33.4 ± 18.6 m) and 2008 (33.2 ± 19.1 m), but that of tertiary caches was shorter in 2007 (43.6 ± 14.1 m) than in 2008 (54.8 ± 28.6 m) (Fig. 3). The dispersal distance of 14 seeds (moved up to 3 times) significantly increased as the seeds were moved from primary caches to tertiary caches ($F_{2,10} = 6.773$, $P = 0.009$).

Part of the cached seeds escaped predation by rodents, but they did not germinate immediately in the next rainy season, and some of them remained dormant for up to 3 years in the caching sites. The proportion of seeds surviving as seedlings was similar between the 2 years (2007, 3.2%, $n = 19$ seeds; 2008, 2%, $n = 12$ seeds) ($Z = 1.595$, $P = 0.207$). During the 2 years, we found 9 seedlings emerged from primary caches, 21 seedlings from secondary caches and 1 seedling from tertiary caches. The dispersal distance of the cached seeds surviving as seedlings ranged from 2 to 121 m, with a mean distance of 32.7 ± 23.5 m.

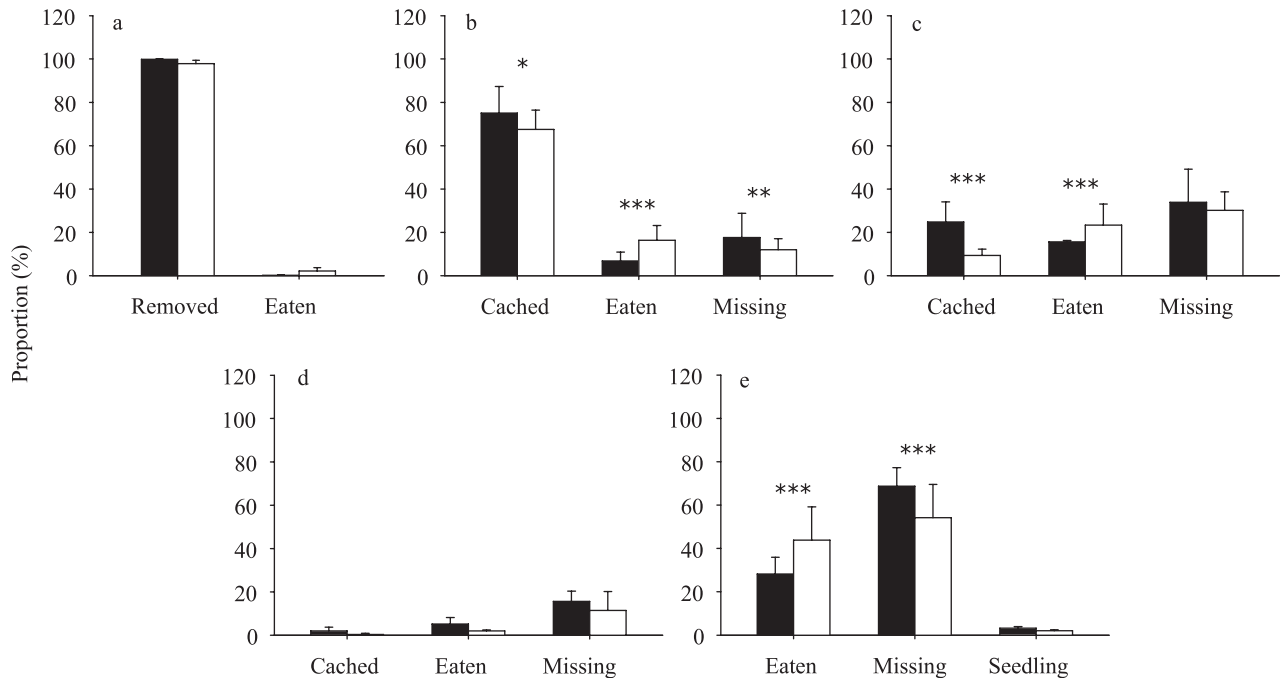


Figure 2 Fate (% mean \pm SD) of the tagged seeds of *Scleropyrum wallichianum* across different dispersal stages in 2007 (■) and 2008 (□): (a) under focal trees, (b) primary dispersal after removal, (c) secondary dispersal after primary caches, (d) tertiary dispersal after secondary caches, and (e) ultimate fate of all tagged seeds. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

Our results support the argument that scatter-hoarding rodents have the potential to improve seed dispersal and subsequent seedling establishment of frugivore-dispersed species such as *S. wallichianum* when large frugivorous vertebrates are in low abundance or locally extinct (see Wright *et al.* 2000; Wright 2003). In the present study, scatter-hoarding rodents removed almost all the tagged *S. wallichianum* seeds and then cached a large portion of them. Moreover, we found that part of the cached seeds survived to germinate and established as seedlings. Previous studies suggest that loss of seed dispersers, caused by human hunting and/or forest fragmentation, might eventually lead to local extinction of tree species that require dispersal by large frugivores (Hamann & Curio 1999; Cardoso da Silva & Tabarelli 2000). However, seed dispersal is far more complex than initially anticipated. Failure of primary dispersal is not equal to failure of dispersal, or even extinction, of a tree species. Ecologically-similar seed dispersers, such as scatter-hoarding rodents in the present study, might compensate or replace large frugivores as seed dispersers (Wright *et al.* 2000; Wright 2003).

The number of *S. wallichianum* seeds that were removed, cached and finally established as seedlings in the present study is similar to that found in other reports on large-seeded species dispersed by scatter-hoarding rodents (e.g. Roth & Vander Wall 2005; Xiao *et al.* 2005a; Xiao & Zhang 2006; Li & Zhang 2007; Moore *et al.* 2007; Gomez *et al.* 2008; Zhang *et al.* 2008; Cao *et al.* 2011). For *S. wallichianum*, large seeds (mean 4.7 g) and hard endocarps might stimulate scatter-hoarding by rodents (Xiao *et al.* 2005b). In addition, we found that cached seeds were buried beneath leaf litters or in the surface soil, and nearly all caches contained only 1 seed. We found that none of the seeds died due to desiccation or any other factors, other than predation by rodents during the experiments. We found that more small caches helped occupy more establishment sites for a given number of seeds and reduced density-dependent mortality, as predicted by the Janzen-Connell model (Janzen 1970; Connell 1971). These caching characteristics are believed to improve seed germination and subsequent establishment (Hollander & Vander Wall 2004; Roth & Vander Wall 2005; Briggs *et al.* 2009).

Dispersal distance of primary caches was farther in 2007 (19.6 ± 14.6 m) than in 2008 (14.1 ± 11.6 m), but the dis-

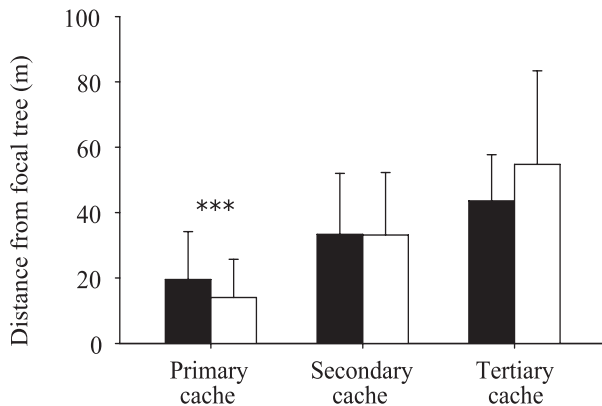


Figure 3 Dispersal distance (mean \pm SD m) of cached seeds from primary, secondary and tertiary caches for *Scleropyrum wallichianum* in 2007 (■) and 2008 (□). *** $P < 0.001$.

tance increased as rodents recovered and moved seeds from primary caches into subsequent caching sites. The dispersal distance reported in the present study was consistent with that reported in many other large-seeded species with scatter-hoarding rodents (e.g. Brewer & Rejmanek 1999; Jansen *et al.* 2004; Xiao *et al.* 2004; Moore *et al.* 2007; Gomez *et al.* 2008; Zhang *et al.* 2008). However, dispersal distance mediated by scatter-hoarding rodents is very limited compared to that by large frugivorous vertebrates (up to hundreds or thousands of meters from the parent plant) (e.g. Fragoso 1997; Westcott *et al.* 2005). Therefore, lack of large frugivores might result in reduced seed dispersal (at least dispersal distance in particular) for frugivore-dispersed plants (Guimaraes *et al.* 2008). With the reduction in primary seed dispersal by large frugivorous vertebrates, the long-term effects of shorter dispersal distance on *S. wallichianum* populations need to be investigated in future.

In conclusion, our results show that as both primary and secondary seed dispersers, scatter-hoarding rodents can play a significant role in maintaining the seedling establishment of *S. wallichianum* and, possibly, other large-seeded fruit trees. We contend that ecologically-similar seed dispersers, such as scatter-hoarding rodents in the present study, might compensate or replace large frugivores as seed dispersers in defaunated forests (Wright *et al.* 2000; Wright 2003). More research is needed to understand to what degree scatter-hoarding rodents and other seed/fruit-eating animals might help maintain the populations of large-seeded fruit species and plant diversity in defaunated forests.

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