



Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest

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Abstract

Few studies have concerned with the differences in seed dispersal, germination and seedling establishment between big and small seeds within a tree species. In this study, the dispersal and fates of big and small nuts (labeled with coded tin-tags) of *Quercus serrata* (a dominant canopy tree species) were monitored at two stands (a primary stand and a secondary stand) in a subtropical broad-leaved evergreen forest in the Dujiangyan Region, Sichuan Province, China. We also examined the differences in germination of big and small nuts of *Q. serrata* without predation by sowing nuts on the ground surface or in the soil. We found that, the big nuts were better survived with longer cache lifetime, longer dispersal distances and higher proportion of emerged seedlings (2% at primary stand, 0.5% at secondary stand) than small nuts. We also found that, there was a marginally physiological difference in germination (germination proportion and seedling height) between big and small nuts. Burial obviously improves germination of both big and small nuts. It is suggested that small rodents may act as an important selective force to affect seed fates, seed shadows and seedling establishment for big and small nut of *Q. serrata*.

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1. Introduction

Besides among plant taxa, seed size variation seems to be very common within plant taxa. Some recent observations have documented that seed size variation has widely existed among large-seeded species (e.g. Forget et al., 1998; Vander Wall, 2001, 2003) and individuals within a tree species (e.g. Brewer, 2001; Jansen, 2003). However, few field observations have concerned with the differences in seed predation and dispersal, germination and seedling establishment

between big and small seeds and nuts within species (e.g. Stanton, 1984, 1985; Brewer, 2001; Jansen et al., 2002; Parciak, 2002a,b; Jansen, 2003). Many seed-dispersed birds and rodents are responsible for the dispersal and fates of many large seeds and nuts (e.g. Price and Jenkins, 1986; Forget and Milleron, 1991; Forget, 1992; Vander Wall, 1990, 2001; Brewer and Rejmánek, 1999; Jansen and Forget, 2001; Theimer, 2001; Zhang and Wang, 2001b). Selection towards seed size by these foraging animals and the consequences of this selection may act as potential selective forces in the evolution of large seed size (Jansen et al., 2002; Vander Wall, 2003).

Large seeds and nuts generally have a higher value, which may largely influence the ways that foraging

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animals treat them after harvest (Jansen et al., 2002; Vander Wall, 2003). There are two opposite predictions about selection of rodents on seed size. The first one is that large seeds might have a lower probability to survive due to higher predation before dispersal (Janzen, 1969, 1971) and higher discovery and pilferage after cached (Stapanian and Smith, 1978; Clarkson et al., 1986; Smith and Reichman, 1984). The second one is that large seeds may have a higher probability to survive since scatter-hoarding animals (e.g. small rodents) store higher-value food (e.g. larger seeds) in lower densities (i.e. further away) to protect them from competitors (Stapanian and Smith, 1978; Clarkson et al., 1986). Recently, some studies indicate that large seeds have a higher probability for seedling establishment due to preferential harvest, improved dispersal and scatter-hoarding (e.g. higher caching proportion and longer dispersal distances) (e.g. Forget et al., 1998; Jansen et al., 2002; Jansen, 2003; Vander Wall, 2003). However, evidences are still not enough to well understand the selective pressures of the above aspects on seed size variation within a plant species (see Brewer, 2001; Jansen et al., 2002; Jansen, 2003).

In this study, we used *Quercus serrata* (a dominant canopy tree species, Fagaceae) as the study species to elucidate the differences in seed dispersal and germination between big and small nuts within the species. *Q. serrata* and other Fagaceae species (e.g. *Q. variabilis*, *Castanopsis fargesii*, *Cyclobalanopsis glauca*, and *Lithocarpus Harlandii*) are distributed in the belt of subtropical broad-leaved evergreen forest (altitude 700–1500 m) in the Dujiangyan Region of Sichuan Province, China. The nut size variation of these Fagaceae species exists among species and individuals within local population (Xiao and Zhang, unpublished data). By following the fates of big and small nuts (labeled with coded tin-tags) of *Q. serrata* at two stands (a secondary stand and a primary stand), we examined whether nut size variation benefit from the selection and caching by small rodents, through investigating the difference of big and small nuts in harvest preference, seed caching (including caching proportion, cache size, dispersal distance, proportion of burial in the soil), survival proportion (i.e. emerged seedlings). And, we also examined the differences in the germination of big and small nuts of *Q. serrata* by sowing seeds on the ground surface or in the soil through excluding predators.

2. Methods

2.1. Study area

This study was performed in an experimental forest (altitude, 700–1000 m) of Dujiangyan city (30°45′–31°22′N, 107°25′–103°47′E), Sichuan Province, China. Climatically, it lies in the middle subtropical zone, with a mean annual temperature of 15.2 °C and an annual precipitation of 1200–1800 mm (Chen, 2000; Chen et al., 2000). The weather is often cloudy and foggy, with only 800–1000 mean annual sunny hours and a mean annual relative humidity of more than 80%.

According to the variation of stand age and vegetation, we selected three stands (over 1500 m apart): a primary stand (80–90 years) and two secondary stands (<50 years). The primary stand (only for seed dispersal experiment) has an area of 2.5 ha. The slope is 30–55° and the aspect is northeast. The canopy trees are *C. fargesii*, *Q. variabilis*, *Q. serrata*, *Pinus massoniana*, *L. harlandii*, *C. glauca*, *Phoebe zhenman* and *Aser catalpifolium*, and most of them produce fruits that ripen during the autumn. Dominant shrubs are *Camellia oleifera*, *Symplocos stellaris*, *S. laurina*, and *Pitosporum daphniphyloides*. The ground flora is poorly developed, consisting of local patches of *Dicranopteris pedata*. One secondary stand was for seed dispersal experiment with an area of 2.0 ha, and its aspect is 25–60° with the direction northeast. And the other was for seed germination experiment with an area of 1.5 ha and its aspect is 25–60° with the direction northeast. In secondary stands, *Q. variabilis*, *Q. serrata* and *C. fargesii* are dominant canopy trees and many of them fruit during the autumn. The under story layer is mainly composed of *S. stellaris*, *S. laurina*, *Ilex purpurea* and *Myrsine africana*. The ground flora is dominated by *D. pedata*.

The flowering period of *Q. serrata* is from March to May and their nut-ripening periods are from September to December (Xiao et al., 2001). *Q. serrata* nuts, like many white oaks (e.g. Griffin, 1971), can germinate soon after falling on the ground, if the temperature and moist are moderate for their germination. In the study site, *Q. serrata* nuts and those of other Fagaceae species and oil tea *C. oleifera* as well as, are consumed and scatter-hoarded mainly by small nocturnal rodents, such as Edward's rats

(*Leopoldamys edwardsi*), Bower's rats (*Berylmys bowersi*), Norway rats (*Rattus norvegicus*), Himalayan rats (*R. nitidu*), Chestnut rats (*Niviventer fulvescens*), Chinese white-bellied rats (*N. confucianus*), (*Apodemus latronum*), Chevriér's field mice (*A. chevriéri*), South China field mice (*A. draco*) and Harvest mice (*Micromys minutus*), among which Edward's rats, Bower's rats, Chestnut rats and Chinese white-bellied rats were dominant species (Xiao et al., 2002). No diurnal rodents (e.g. squirrels) were found in the study site. Granivorous birds, i.e. Eurasian jay (*Garrulus glandarius*), were observed to forage nuts of *Q. serrata*, *Q. variabilis*, *C. fargesii* and *C. glauca* in the canopy of forest. They seldom forage nuts on the ground and the number of them is very few (Xiao, 2003).

2.2. Nut collection and preparation

All experiments were conducted from November 2000 to May 2001. We randomly collected fresh ripe nuts of *Q. serrata* on the ground surface and stored them under room temperature (about 15–20 °C) in the laboratory (for 2 weeks). Only sound nuts were used in this study. We sorted sound nuts into two categories: big and small nuts and measured each nut category for diameter, length, fresh nut weight and kernel weight by randomly sub-sampling ($n = 60$ for each category). Then, we randomly selected 400 nuts each nut categories and labeled them with a small, light tin-tag (4 cm × 1 cm, <0.1 g) through the hole (0.5 mm in diameter, near the germinal disc of a nut with an electrical drill) by using a thin steel wire 8 cm long (Zhang and Wang, 2001b; Li and Zhang, 2003). Each tag was coded using a sharpened metal-pen with a serial number to make every seed identifiable. If rodents bury the tagged seeds in the soil, the tin-tags are often left on the surface (nearly 100%), making them easy to relocate. Tagging has a negligible effect on seed removal and caching by rodents (Zhang and Wang, 2001b).

2.3. Seed dispersal experiment

A plot was selected at each stand. The 20 successive sites were distributed along each plot as experimental seed stations, and spaced 8–12 m apart. At each seed station, a bamboo stick (15 cm × 1.5 cm) was set up

and numbered serially from 1 to 20. On 13 November 2000 (secondary stand) and 20 November 2000 (primary stand), we released 10 tagged nuts each category at each seed station. After seed release, we checked the tagged nuts at each seed station to investigate nut harvest and removal by small rodents and recorded their fates. At the same time, we randomly searched the area around each seed station (radius, ≤ 20 m) with equal efforts. We frequently checked all the seed stations and their surrounding area and all cache sites relocated in previous visits as well. We recorded the relevant information of the relocated nuts. When we found a cache, we recorded their caches and seed code numbers, measured the distance of the tagged nuts or their fragments to their original seed stations and determined the cache location using a bamboo stick that was coded with the numbers of nuts in indelible ink. The sticks were set 10 cm away from the seed caches. The marked sticks or seed number checking might give rodents some cues for pilfering, although, we attempted to keep the disturbance of the caches to a minimum. In the next visit, we also checked all the caches relocated in previous visits until the caches were removed or eaten by rodents. If a marked cache was removed, the area around the cache (radius, ≤ 10 m) was randomly searched. We surveyed all previously found cache sites and newly found cache sites to determine which site had surviving seeds the following spring on 29 April (at secondary stand) and 1 May (at primary stand) of 2001.

2.4. Seed germination experiment

Nut positions (on the ground or in the soil) cached by rodents often affect the seed germination (Vander Wall, 1990, 1993). It is necessary to see if there is difference in germination of big and small nuts on the ground and in soil. We randomly selected 400 big nuts and 400 small ones for seed germination. In a secondary stand, 20 sites were randomly selected and spaced 8–10 m apart. In each site, an enclosure with an area of 1 m² was set up to protect the sowed nuts from small rodents and birds, but free to insects using 10 mm mesh wire. Ten nuts for each nut category were buried 10–40 mm (similar depth as rodents do) in the soil and 10 nuts for each nut category were sowed on the soil surface with some leaf litter (800 nuts, 20 enclosures × 2 sowed positions × 2 nut categories) on

10 November 2000. The nuts were distributed evenly in each enclosure to reduce the effects of seed density on seed germination and seedling emergence. On 2 May 2001, we investigated the emergence of seedlings and measured their height.

2.5. Data analyses

All statistical analyses were conducted with the SPSS 10.0 statistical package. Mann–Whitney test was used to compare the differences of nut characters between nut categories related to diameter, length and fresh nut weight and kernel weight.

For seed dispersal and fates, data were analyzed with a fully crossed ANOVA with two fixed effects of nut category (big and small) and stand (primary and secondary stands) and a random effect of depot nested within stand (also see Sork, 1987; Forget, 1992 for similar analysis). To attain normality, the proportion of nut final removal at each seed station and that of nut cache from each seed station (only for primary caches) were arcsin-transformed and dispersal distances were \log_{10} -transformed. Analyses of nut survival at seed stations and survival of cached nuts at cache sites (including primary and secondary caches) were performed using Cox model (Muenchow, 1986). Cox model was also used to compare the difference of the lifetime of seed stations between big and small nuts, and independent-sample *T*-test was used to further verify whether small rodents have some preference to nut size during the harvesting phase. Two-tailed χ^2 -test was used to compare the differences of frequency distributions of cache size (i.e. one-nut caches versus two- and three-nut caches, including primary and secondary caches) between nut categories and between stands. We also used two-tailed χ^2 -test to compare the differences in emerged seedlings and the

tagged nuts buried in the soil by small rodents between big and small nuts.

For seed germination, data were also analyzed with a fully crossed ANOVA with two fixed effects of nut category (big and small) and sowed position (in the soil and on the soil surface). The proportion of seedlings emerged from each treatment in each enclosure was arcsine-transformed and seedling height was \log_{10} -transformed.

3. Results

3.1. Nut categories

For all four types of nut characters: diameter, length, fresh nut weight and kernel weight, the difference of mean size was very significant between big and small nuts (all $P < 0.001$, Table 1). For example, mean weight of either fresh nut or kernel of big nuts was as nearly twice as that of small nuts (Table 1).

3.2. Seed dispersal and seed fates

Since, birds often forage nuts on the canopy and the number of them is very few, nut removal on the ground after release are assumed to be caused by small rodents. Both big and small nuts were removed rapidly at both stands after release. As shown in Fig. 1 and Table 2, the total proportion of nut removal showed no difference between big and small nuts after release; the proportion of seed removal was 58.5% (117/200) for big nuts and 57.5% (115/200) for small nuts at primary stand and 71.5% (143/200) for big nuts and 75.0% (150/200) for small nuts at secondary stand. The rest were consumed in situ. The difference of nut removal at each seed station was not significant

Table 1
Characteristics of big and small *Q. serrata* nuts used for seed dispersal and germination experiments

Nut characters	Mean \pm S.D.		Mann–Whitney test (<i>P</i>)
	Big nuts (<i>n</i> = 60)	Small nuts (<i>n</i> = 60)	
Diameter (mm)	10.8 \pm 1.3	8.7 \pm 0.8	0.001
Length (mm)	20.0 \pm 2.2	17.3 \pm 2.3	0.001
Nut weight (g)	1.46 \pm 0.29	0.78 \pm 0.15	0.001
Kernel weight (g)	1.20 \pm 0.32	0.67 \pm 0.26	0.001

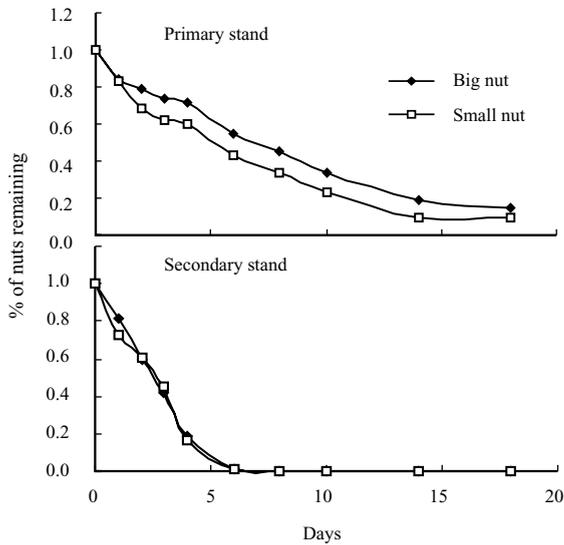


Fig. 1. Survival of big and small *Q. serrata* nuts at seed stations over 18 days at both stands.

between nut categories (ANOVA: $F_{1,78} = 0.034$, $P = 0.855$), but the removal in secondary stand was significantly higher than in primary stand (ANOVA: $F_{1,78} = 5.022$, $P = 0.028$). There was no interaction on nut removal between nut size and stand (ANOVA: $F_{1,78} = 0.109$, $P = 0.742$). There was very small difference of lifetime at seed stations between big and small nuts at either stand (Cox model, $P > 0.05$), but the lifetime of both nut categories were significantly longer at primary stand than that in secondary stand (Cox model, $P < 0.05$). There was also no difference of lifetime of seed stations between big and small nuts at either stand by using both Cox model ($P > 0.05$) and independent-sample *T*-test ($P > 0.05$).

After removed from seed stations, the fates of the tagged nuts can be sorted into three categories: cached (including buried in the soil and deposited on the soil surface), eaten leaving only tin-tags and seed fragments (eaten) and missing with their true fates unknown (missing) (Fig. 2). For either nut category, less than 10% of nuts were cached by small rodents at both stands. There was no difference in nut cache proportion from each seed station either between nut categories (ANOVA: $F_{1,78} = 0.091$, $P = 0.764$) or between stands (ANOVA: $F_{1,78} = 0.204$, $P = 0.653$) and also no interaction between nut size and stand (ANOVA: $F_{1,78} = 0.204$, $P = 0.653$). Almost big and small nuts removed from seed stations were eaten or missing at both stands (Fig. 2). The missing nuts might be transported into underground burrows, rock caves and dense shrubs, or beyond the survey area. In the following spring (May), the proportion of emerged seedling from big nuts (2.0%, 4/200) was significantly higher than that from small nuts (no seedlings) at primary stand ($\chi^2 = 4.040$, d.f. = 1, $P = 0.040$), but slightly higher at secondary stand (big nuts, 0.5%, 1/200; small nuts, no seedlings; $\chi^2 = 1.003$, d.f. = 1, $P = 0.317$) (Fig. 2). The lifetime of the cached big nuts was significantly longer than that of the cached small nuts at secondary stand ($\chi^2 = 5.496$, d.f. = 1, $P = 0.019$), but a little longer at primary stand ($\chi^2 = 1.428$, d.f. = 1, $P = 0.001$) (Table 2). The lifetime of the cached nuts at primary stand was significantly longer than that at secondary stand for small nuts ($\chi^2 = 13.207$, d.f. = 1, $P = 0.001$) (Table 2). There was no much difference in total proportion of buried nuts by rodent between big nuts (50%, $n = 20$) and small nuts (86.7%, $n = 15$) at primary stand (d.f. = 1, $P = 0.308$); between big nuts (76.5%,

Table 2

Mean lifetime of the tagged nuts at seed stations and at primary + secondary caches in both stands

	Big nuts		Small nuts	
	Mean \pm S.D.	<i>n</i>	Mean \pm S.D.	<i>n</i>
Primary stand				
Seed stations	8.9 \pm 6.0	200	7.2 \pm 5.5	200
Primary + secondary cache	125.7 \pm 52.2	20	100.3 \pm 71.4	14
Secondary stand				
Seed stations	3.2 \pm 1.8	200	3.1 \pm 1.8	200
Primary + secondary cache	57.6 \pm 76.9	15	3.9 \pm 3.7	15

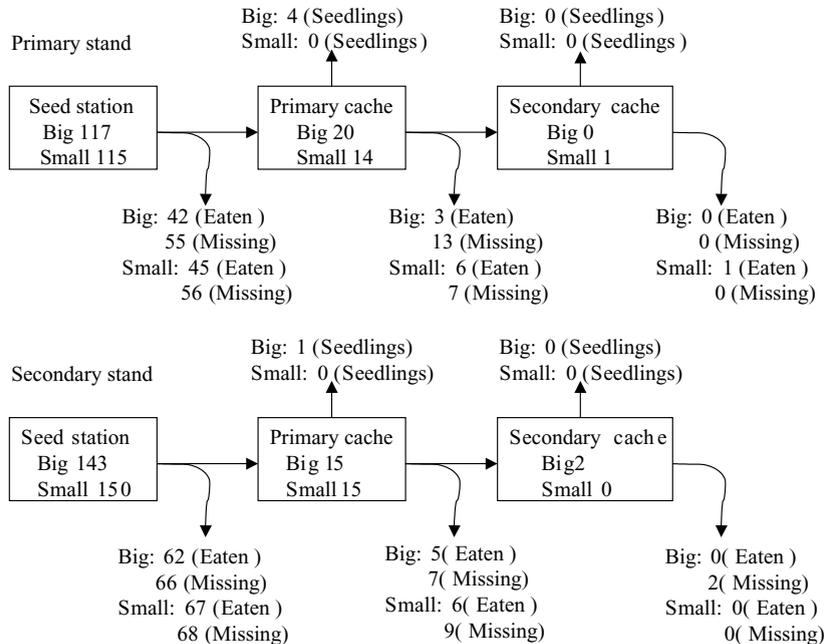


Fig. 2. Post-dispersal fates of big and small nuts of *Q. serrata* removed from seed stations by small rodents at both stands.

$n = 17$) and small nuts (73.3%, $n = 15$) at primary stand (χ^2 -test, d.f. = 1, $P = 0.938$).

Most (over 90%) of caches contained only one nut for either nut category or stand. One primary cache contained three big nuts and two *C. fargesii* nuts at primary stand, and another primary cache had one big nut and one *C. glauca* nut at secondary stand. The difference of frequency distributions between one-nut caches and two-nut + three-nut caches was not significant either between nut categories or between stands ($P > 0.05$). Mean nut number per cache (i.e. cache size) was 1.1 ± 0.3 ($n = 16$) for big nuts and 1.2 ± 0.6 ($n = 13$) for small nuts at primary caches and 1.3 ± 0.6 ($n = 16$) for big nuts and 1.0 ± 0.0 ($n = 15$) for small nuts at secondary stand.

Over 80% of the tagged nuts (for either nut category) were cached 0.0–10.0 m away from seed stations at both stands (Fig. 3). The maximum dispersal distances of cached seeds were 10.8 m for big nuts and 8.0 m for small nuts at primary stands and 28.5 m for big nuts and 4.7 m for small nuts at secondary stands. The dispersal distances of big nuts were significantly longer than those of small nuts (ANOVA: $F_{1,65} = 9.340$, $P = 0.003$), but the dispersal distance of nuts was not significantly longer at primary stand than at

secondary stand (ANOVA: $F_{1,65} = 0.055$, $P = 0.815$) and there was no interaction between nut category and stand (ANOVA: $F_{1,65} = 0.486$, $P = 0.488$) (Figs. 3 and 4). Only one small nut at primary stand and two big nuts at secondary stand were transported from primary caches to secondary caches (Fig. 2).

The big nuts (50.0%, 10/20) buried in the soil (ca. 10–40 mm, including primary and secondary caches) was much lower than small nuts (86.7%, 13/15) at primary stand (χ^2 -test, d.f. = 1, $P = 0.308$), but similar at secondary stand (big nuts, 76.5% (13/17); small nuts, 73.3% (11/15) (χ^2 -test, d.f. = 1, $P = 0.938$), while the rest were deposited on the soil surface with some leaf litter covering.

3.3. Seed germination in exclosures

The proportion of seedlings emerged was slightly higher for small nuts than for big nuts with approximate significance (ANOVA: $F_{1,78} = 3.228$, $P = 0.076$). The proportion of seedlings emerged from buried nuts in the soil were significantly higher than that on the ground (ANOVA: $F_{1,78} = 36.319$, $P = 0.001$) (Table 3). There was no interaction of seed germination between nut size and sowed position (ANOVA: $F_{1,78} = 0.462$,

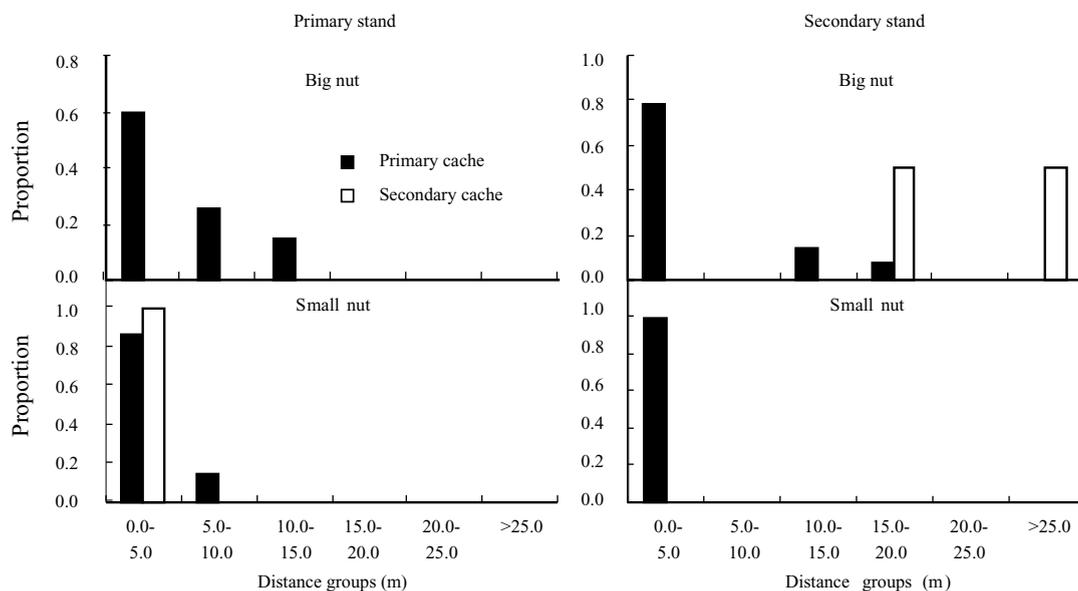


Fig. 3. Frequency distributions of dispersal distances of the tagged seeds in primary + secondary caches from seed stations at both stands.

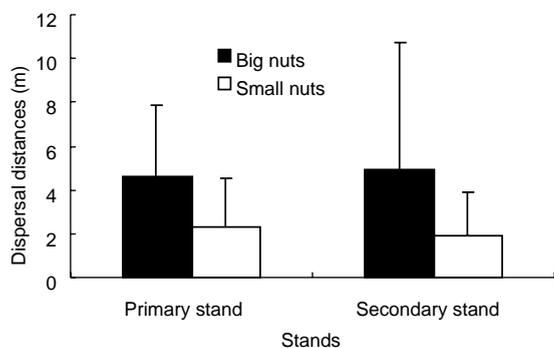


Fig. 4. Mean dispersal distances (m) of the nuts in primary caches at both stands.

$P = 0.499$) (Table 3). There was no difference in seedling height between big and small nuts (ANOVA: $F_{1,542} = 2.316, P = 0.129$), no difference in seedling height between sowed positions (ANOVA: $F_{1,542} = 0.007, P = 0.935$) and no interaction (ANOVA: $F_{1,542} = 0.166, P = 0.684$) (Table 3).

4. Discussion

In this study, we found that, there were differences in lifetime, dispersal distance and emerged seedlings between big and small cached nuts. Big nuts with longer lifetime, longer dispersal distance and higher proportion of emerged seedlings tended to be better survived than small nuts, indicating big nuts has

Table 3

Germination of big and small nuts of *Q. serrata* in the exclosures protecting from rodents and birds under two sowed positions: burial 10–40 mm in the soil and sowing on the soil surface ($n = 200$ for each treatment)

Nuts	Sowed positions	Seedling emergence (%)		Seedling height (cm)	
		Mean \pm S.D.	n	Mean \pm S.D.	n
Big	Burial	78.0 \pm 24.0	20	11.5 \pm 3.7	157
	Surface	47.5 \pm 28.8	20	11.4 \pm 4.1	98
Small	Burial	87.0 \pm 21.8	20	11.0 \pm 4.3	174
	Surface	57.0 \pm 23.2	20	11.0 \pm 3.7	115

advantages over small nut under selection of small rodents. The observation of rodents transported big nuts to longer distances than small nuts coincides well with many previous observations based on intraspecific seed size (e.g. Hurlly and Robertson, 1987; Jansen et al., 2002; but just the reverse Brewer, 2001), and on interspecific seed size as well (e.g. Stapanian and Smith, 1984; Vander Wall, 1995b, 2003; Forget et al., 1998; Xiao and Zhang, unpublished data). According to models of optimal cache spacing (Stapanian and Smith, 1978; Clarkson et al., 1986), seed-caching birds and rodents tend to scatter-hoard higher-value food far from the seed source to protect it from competitors. Meanwhile, some cached seeds is moved into new cache sites, which further extended the distances of caches from the seed source and the intercache distances (e.g. between primary and secondary caches) (e.g. Vander Wall, 1995a, 2002; Xiao, 2003). Increased dispersal distances can avoid strong seed predation under parent trees (e.g. Janzen, 1969, 1971). This may be the important reason that big nuts have a higher survival rate after dispersal by small rodents.

There were no differences in proportion of cached nuts, proportion of buried nuts, cache size, harvest or removal speed at seed station. The observation that small rodents have little preference to harvest and remove both big and small nuts of *Q. serrata* at both stands (Fig. 1 and Table 2) supports the result obtained by Jansen et al. (2002), but not support several previous observations (e.g. Janzen, 1969, 1971; Harper, 1977; Brewer, 2001). The reasons of non-selection by rodents are not well understood. Seed size may be a relatively less important character for some large-seeded species (e.g. *Q. serrata* in this study) to foraging animals due to few other differences (but seed mass) among them. Local food availability may be another important limiting factor to non-selectivity by small rodents (Jansen et al., 2002). Jansen (2003) has observed that acouchies were indeed size-selective during seed harvesting under ambient seed abundance, but this condition did not occur in this study probably because the seed abundance was not very rich when the experiment was conducted near the end of seed rain of *Q. serrata* and other species (mid-November). In addition, small rodents are highly sensitive to seed perishability (e.g. early germination of acorns of white oak species) (e.g. Hadj-Chikh et al., 1996; Smallwood et al., 2001; Steele et al., 2001), which may influence

their decisions to cache and consume. This may be another reason that small rodents showed no preference to harvest *Q. serrata* nuts (either big or small), which germinate soon after they fall on the ground in the study site.

Generally, big nuts contain more nutrient reserves for seed germination and early growth of seedlings than small nuts (e.g. Harper et al., 1970; Westoby et al., 1992; Leishman et al., 2000). Therefore, big nuts have a greater probability to germinate and establish a seedling (e.g. Stanton, 1984, 1985). But this conclusion was not supported by our study. In this study, there was a marginally physiological difference in germination (germination proportion and height of seedling) between big and small nuts. For both nut categories, the proportion of germination of buried nuts was significantly higher than that of unburied nuts, supporting the general observations that burial of seeds by small rodents would benefit seed germination and seedling establishment (e.g. Shaw, 1968; Griffin, 1971; Boucher, 1981; Borchert et al., 1989; Vander Wall, 1990, 1993; Zhang, 2001; Zhang and Wang, 2001a). Most large seeds are often buried 0–60 mm in the surface soil by seed-caching birds and rodents (e.g. Vander Wall, 2002, 2003, 1990, 1993), though a small part of them are deposited on the soil surface (like this study). Seeds benefit from burial by hoarding animals through the reduction of seed predation, the maintenance of seed viability in a favorable condition, the increase of seedling establishment and facilitation to penetrate the ground for roots of buried seeds (Vander Wall, 1990, 1993; Jansen and Forget, 2001, Xiao and Zhang, personal observation).

In brief, small rodents may act as an important selective force to affect seed fates, seed shadows and seedling establishment for big and small nuts of *Q. serrata* in the study area. Big nuts could benefit more than small ones from seed dispersal and caching with longer cache lifetime, longer dispersal distances and higher proportion of emerged seedlings. However, because the relative small sample size of cached nuts (especially the proportion of emerged seedlings), this observation need further study.

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