Original article

# Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species

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## Abstract

We studied the effect of seed size on dispersal by comparing dispersal distances in five rodent-dispersed fagaceous species (*Lithocarpus harlandii, Quercus variabilis, Q. serrata, Cyclobalanopsis glauca, Castanopsis fargesii*) with different seed size. We tracked individual seeds with coded tin-tags in two stands over 3 years in a subtropical evergreen broadleaved forest in the Dujiangyan Region of Sichuan Province, Southwest China. Our seed tracking data indicate that dispersal distances (including mean, maximum and distribution range) of seeds in primary caches and of seeds eaten after dispersal significantly increased with seed size, for both stands and all years. In addition, larger seeds (*L. harlandii* and *Q. variabilis*) were re-cached more often than smaller ones, which further reduced the relative density among caches and extended dispersal distances. Our findings indicate that greater dispersal distances for larger seeds might benefit the evolution of differences in seed size, and that scatter-hoarding might be advantageous for rodent-dispersed tree species.
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*Keywords:* Large seed size; Seed dispersal; Dispersal distance; Scatter-hoarding by rodents

## 1. Introduction

It is poorly understood why there is an enormous variation in seed size (up to 10 orders of magnitude) among vascular plant species (Harper et al., 1970). Seed size plays a vital role in plant life history (Venable and Brown, 1988; Westoby et al., 1992,1996; Gómez, 2004), such as seed production (e.g. Parciak, 2002a,2002b), seed predation (e.g. Kollmann et al., 1998; Moles et al., 2003), seed dispersal (e.g. Levey, 1987; Greene and Johnson, 1993; Jordano, 1995; Forget et al., 1998; Brewer, 2001; Jansen et al., 2002,2004; Vander Wall, 2003; Theimer, 2003; Xiao et al., 2004a), seed germination and early growth of seedlings (e.g. Yanful and Maun, 1996; Seiwa et al., 2002; Paz and Martlnez-Ramos, 2003), and plant communities (e.g. Eriksson and Jakobsson, 1999; Leishman, 2001). Smith and Fretwell (1974) reasoned that plants must find an optimal trade-off between producing large seeds and producing many seeds due to the limiting resources for reproduction, and also that dispersibility (including dispersal distances) of the seeds decreases with increasing seed size. The negative relationship between dispersibility and seed size holds for many plant species (e.g. Baker, 1972; Augspurger, 1986; Levey, 1987; Greene and Johnson, 1993; Jordano, 1995; Benkman, 1995; Sakai et al., 1998), but seems not to hold for large-seeded plant species primarily dispersed by seed-caching rodents (Jansen et al., 2002,2004).

After they shed from the parent tree, seeds are often differentially removed, consumed and scatter-hoarded by seed-eating rodents, mainly depending on seed size and other seed traits (Price and Jenkins, 1986). Larger seeds and nuts generally have a greater nutritional value for rodents than smaller ones, and may, therefore, be more attractive for them to cache as food reserves (e.g. Smith and Reichman, 1984; Jansen and Forget, 2001; Jansen et al., 2002,2004) or eat (e.g. Janzen, 1969,1970; Moles et al., 2003). According to the optimal cache spacing model, caching effort represents a trade-off between the costs of transporting and hiding seeds, and the costs of distance- or density-dependent cache loss (Stapanian and Smith, 1978,1984; Clarkson et al., 1986). Therefore, one important prediction of the optimal cache spacing model is that scatter-hoarding animals store higher-value food

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(e.g. larger seeds) in lower densities (i.e. further away) to protect them from competitors (see also Vander Wall, 1990). Moreover, the distribution of the dispersed seeds around the seed source generally conforms to a negative exponential curve (Sork, 1984). In addition, larger seeds are more likely to be recovered and re-cached into a further cache site (Vander Wall and Joyner, 1998; Jansen et al., 2002, 2004; Vander Wall, 2003; Xiao et al., 2004a). However, it is still not well understood how interspecific seed size influences seed dispersal by seed-caching rodents (e.g. Forget et al., 1998; Vander Wall, 2003).

We studied the relationship between seed size and dispersal distance using five rodent-dispersed fagaceous species with different seed size: *Lithocarpus harlandii, Quercus variabilis, Q. serrata, Cyclobalanopsis glauca* and *Castanopsis fargesii*. We tracked individual seeds with coded tin-tags in two stands (primary stand and secondary stand) over 3 years in a subtropical evergreen broadleaved forest in the Dujiangyan Region of Sichuan Province, Southwest China. In this study, we test whether the dispersal distance of seeds dispersed by seed-caching rodents increases with seed size. We also investigated the potential effects of other seed traits on seed size and dispersal distance.

## 2. Methods

### 2.1. Study site and study species

From November 2000 to April 2003, we carried out this study in the Banruosi Experimental Forest (altitude 700–1000 m, 31°4′N, 103°43′E) of Dujiangyan City, Sichuan Province, Southwest China. The site 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). The weather is often cloudy and foggy, with annual hours of sunlight typically in the range 800–1000 and a mean annual relative humidity of more than 80%.

Subtropical evergreen broadleaved forest (elevation, 700–1500 m) in the Dujiangyan Region of Sichuan Province, China are a mosaic often isolated and fragmented by agricultural development resulting in populations of many otherwise common tree species being very rare or even extinct due to logging (Chen, 2000). The Experimental Forest chosen for this study is mainly dependant on natural regeneration of native tree species though modern human interference has greatly influenced its regeneration. The variation in stand age and vegetation structure provided natural divisions into three stand types: primary stands (>80–90 years), secondary stands (<50 years) and shrublands (<10 years). In order to see whether the effects of seed size on dispersal are independent of environmental factors (e.g. stand and seed availability), we selected a secondary stand and a primary stand to conduct the seed dispersal experiment (see Xiao et al., 2004a, 2005). The stands were about 4 km apart. The secondary stand (1.5 ha) was 40–50 years old, the slope was 20–40° and the direction was northeast. In this stand, *Q. variabilis, Q. serrata*, and *C. fargesii* were the dominant canopy tree species, but few individuals of *L. harlandii* and *C. glauca* remained due to logging. The understory layer was mainly composed of *Symplocos stellaris, S. laurina, Ilex purpurea*, and *Myrsine africana*. The ground flora was dominated by *Dicranopteris pedata*. The primary stand (2 ha) was over 80–90 years old, the slope was 35–60° and the direction was west. The dominant tree species were *C. fargesii, Q. variabilis, Pinus massoniana* (Pinaceae) and *Acer catalpifolium* (Aceraceae), with a small population of other tree species *Q. serrata, L harlandii, C. glauca* and *Phoebe zhenman* (Lauraceae). Dominant shrubs were *Camellia oleifera, S. stellaris, S. laurina*, and *Pittosporum daphniphylloides*. The ground flora was poorly developed, consisting of local patches of *D. pedata*.

The study species, *L. harlandii, Q. variabilis, Q. serrata, C. glauca* and *C. fargesii*, co-occur naturally in the study site, and the main seed rain periods of these trees species strongly overlap in October, with little difference in peak time (Xiao et al., 2001; Xiao, 2003; Z-S Xiao, personal observation). The five fagaceous species showed considerable variation in seed size as the ratio of the large nuts of *L. harlandii* to those of *C. fargesii* is up to 10 (Table 1). Since these five nuts come from the same family with similar nutrient composition (i.e. protein, fat and starch) and caloric value, seed size seems reasonably to reflect potential food value for seed-eating rodents, compared with other seed traits (e.g. seed coat

Table 1
Some morphological and ecological traits of the fagaceous study species. Seed chemical analyses were conducted in duplicate on a mixture of sound seeds (*n* = 50–100) for each seed species. Data of seed chemical compositions (i.e. protein, fat, starch and tannin) in dry nut meat were provided by Center of Grain Quality of Ministry of Agriculture, China, and caloric value of dry nut meat was measured by Bomb Calorimeter (PARR 1281) in the Institute of Zoology, CAS. Species are ordered after seed mass. All seed species were leathery and dispersed by rodents and birds, except *L. harlandii* with a hard seed coat only dispersed by rodents. Protein, fat, starch, tannin and caloric are represented in % dry nutmeat from mixed 50–100 nuts per species. Main potential dispersers are seed-eating rodents, e.g. Edward's long-tailed rats (Xiao et al., 2003)

| Species | Fruiting | Fresh seed mass (g) | Dry seed mass (g) | Protein (%) | Fat (%) | Starch (%) | Tannin (%) | Caloric (J/g) |
|---|---|---|---|---|---|---|---|---|
| *L. harlandii* | October–December | 4.56 | 3.14 | 5.80 | 0.91 | 37.66 | 1.34 | 17.11 |
| *Q. Variabilis* | September–December | 2.42 | 1.71 | 5.92 | 3.94 | 54.17 | 11.7 | 17.63 |
| *Q. Serrata* | September–December | 0.97 | 0.77 | 6.07 | 3.02 | 54.01 | 10.6 | 17.26 |
| *C. glauca* | October–December | 0.95 | 0.47 | 4.80 | 1.88 | 55.42 | 11.1 | 17.00 |
| *C. fargesii* | October–December | 0.46 | 0.31 | 4.90 | 1.22 | 67.65 | 0.2 | 17.03 |

and tannin). Therefore, we hypothesize that seed dispersal by seed-caching rodents is influenced mainly by seed size for these five fagaceous species.

Eleven rodent species coexisted in the study site: Edward's long-tailed rats (*Leopoldamys edwardsi*, 200–500 g), Bower's rats (*Berylmys bowersi*, 200–400 g), Norway rats (*Rattus norvegicus*, 100–200 g), Himalayan rats (*R. nitidus*, 100–200 g), chestnut rats (*Niviventer fulvescens*, < 100 g), Chinese white-bellied rats (*N. confucianus*, < 100 g), Sichuan field mice (*Apodemus latronum*, < 30 g), Chevrier's field mice (*A. chevrieri*, < 70 g), South China field mice (*A. draco*, < 30 g), striped field mice (*A. agrarius*, < 50 g) and harvest mice (*Micromys minutus*, < 10 g) (Xiao et al., 2002; Z-S Xiao, unpublished data). All are small and nocturnal. Edward's long-tailed rats, Bower's rats, chestnut rats, Chinese white-bellied rats and Himalayan rats are dominant or common species (Xiao et al., 2002; Xiao, 2003). These rodents were the main seed-eaters of the large-seeded study species with marked preference for *C. fargesii* and *L. harlandii* over *Q. variabilis*, *Q. serrata* and *C. glauca* with higher tannin concentrations by feeding and field observations (Xiao et al., 2003a; Xiao and Zhang, 2004), and at least Edward's long-tailed rats were found to scatter-hoard the tree seeds in outdoor arenas (2 × 2 m) (Xiao et al., 2003a). Previous studies suggested that these rodents were likely to affect natural regeneration of the large-seeded tree species (Xiao et al., 2001, 2003a, 2003b, 2004a, 2004b, 2005). Several bird species, notably the Eurasian jay *Garrulus glandarius*, were also seed predators and potential seed dispersers, but they have small populations and may contribute relatively little to forest regeneration. Moreover, these birds seldom forage on the ground under the canopy (see Den Ouden et al., 2004), and never feed the marked seeds according to the fragments of the eaten seeds during this study (Z-S Xiao, personal observation).

## 2.2. Seed dispersal experiment

Mature, fresh target tree seeds were collected from the ground outside the experiment sites 1 or 2 weeks before the seed dispersal experiment. Each year, we randomly selected 400 sound seeds for each tree species (no *C. fargesii* seeds were available in 2002 due to a poor seed crop), and labeled them (total, 5600 seeds) using the methods by Zhang and Wang (2001) with some small modifications. A tiny hole 0.5 mm in diameter was drilled near the germinal disc of each seed. Though the cotyledons were partly damaged (except for *L. harlandii* nuts), the embryo remained intact and was capable of germinating. A small, light tin tag (3.5 × 1 cm, < 0.1 g) was tied through the hole using a thin steel wire 8 cm long. Each seed was given a unique number by writing on the tag using a fine point metal-pen. When rodents buried the seeds in the soil, the tin-tags were often still on the surface, making them easy to relocate.

In both the primary and the secondary stands, 20 plots (ca. 1–1.5 m$^2$ per plot) were established as experimental cafeteria stations along a transect line, and spaced 10 m apart. In November each year (2000, 2001 and 2002), we placed 50 tagged seeds (10 seeds for each seed species) at each cafeteria station. The following day after place, we checked the tagged seeds at each station to record removal. At the same time, we randomly searched the area around each station (radius, over 20 m) with equal efforts (3–4 h for two people each visit), for the tagged seeds and their fragments to record seed fate. The checking frequency was similar for each year, that is, 1 d, 2 d, 3 d, 4 d, 6 d, 8 d, 12 d, 16 d, 24 d, 32 d, 48 d, 160–170 d (next April). The relevant information of the relocated seeds was recorded. Post-dispersal seed fates can be sorted into three categories: (1) "cached", i.e. buried intact in the soil and deposited intact on the surface; (2) "eaten", i.e. leaving only tin-tags and seed fragments; and (3) "missing", i.e. not retrieved within the search area, hence with unknown fate. When we found a cache, we carefully exposed the seeds, recorded their caches and seed code numbers, and measured the distance of the tagged seeds or their fragments to their original seed stations. We then reburied the seeds in the cache site as they were made by rodents and attempted to keep the disturbance of the caches to a minimum. In order to determine the spatial-temporal variation in the fate of seeds cached by small rodents, we used a bamboo stick (15 × 1.5 cm), which was coded with the number of the relocated seed, to determine the cache location [Note: 55 days after establishing artificial caches in autumn 2003, we found that tin-tags and marked sticks have had little effect (*G*-test, *G* = 1.959, df = 2, *P* = 0.375) on seed removal from artificial caches among these three treatments: one-tagged seed with a marked stick, 10%; one-tagged seed, 14%; one untagged seed, 20% (*n* = 50 replications per treatment, Z-S Xiao and Z-B Zhang, unpublished data)]. 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, at least 10 m) was randomly searched. When a seed in a primary cache or higher order cache (e.g. secondary cache) was removed and found in another cache site, we measured the distance to the original seed source and also the distance to its previous cache.

## 2.3. Data analysis

Three-factor ANOVA was used to test the differences in dispersal distances (log$_{10}$-transformed to meet normality) of the cached seeds in primary caches and the eaten seeds (i.e. seed fragments) after dispersal from cafeteria stations with seed species, stand and year as the between-subject effects, including all possible interactions. Typically, we did not retrieve all of the seeds that animals removed from the plots. In order to see whether the missing seeds can be excluded without biasing the results, Three-factor ANOVA was also used to test the difference in dispersal distances with seed fate (i.e. cached vs. eaten), stand and year as the between-subject effects, including all possible interactions for each species. For all the data across stands and years, Pearson's

correlation was used to analyze the relationships between seed fresh weight and the proportion of seeds relocated (arcsin-transformed to meet normality). By pooling the data across stands and years (because of small sample sizes within plots for plot-level analysis), stepwise linear regression was used to determine which seed trait (including fresh seed weight, dry seed weight, protein, fat, starch, crude fiber, tannin, and calories in Table 1) are correlated with dispersal distances, but we excluded the seed coat hardness in regression analysis because we found it difficult to quantify.

## 3. Results

During the 3 years survey, we relocated 42.5% of the tagged seeds in the primary stand and 39.2% in the secondary stand after they were dispersed from cafeteria stations. The proportion of seeds relocated was strongly negatively correlated with seed fresh weight in the secondary stand ($r = -0.807$, $n = 14$, $P < 0.001$; Fig. 1b), but not significantly in the primary stand ($r = -0.434$, $n = 14$, $P = 0.121$; Fig. 1a). Among the relocated seeds, the proportion of seeds cached was 51.4% (395 seeds) in the primary stand and 24.8% (198 seeds) in the secondary stand.
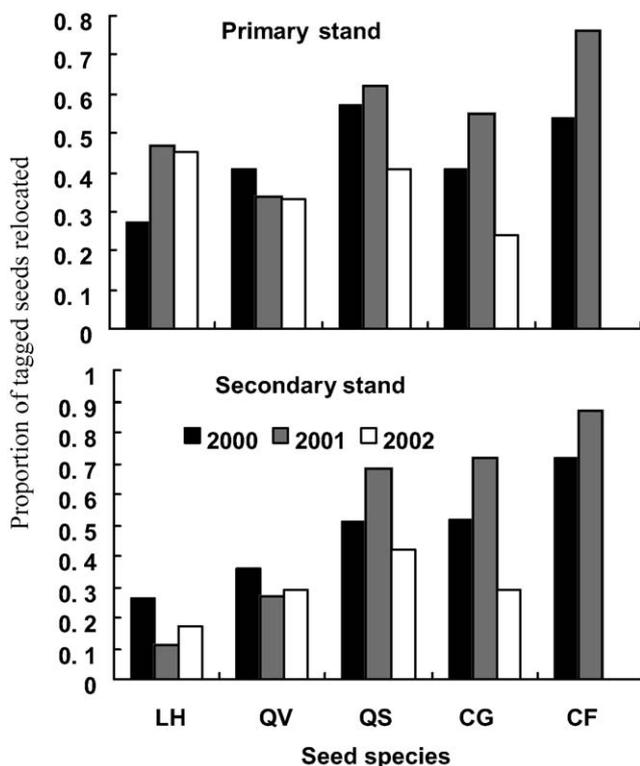


Fig. 1. Relationship between seed size and the proportion of tagged seeds relocated of five fagaceous species after dispersed from cafeteria stations: (LH) *L. harlandii*, (QV) *Q. variabilis*, (QS) *Q. serrata*, (CG) *C. glauca*, and (CF) *C. fargesii*.

## 4. Frequency distributions of dispersal distances

In both stands, and both for cached seeds and eaten seeds post-dispersal distance to the source increased with seed size (Fig. 2): *L. harlandii* seeds (the largest ones) had an relatively even distribution with the longest tail; *Q. variabilis* seeds (the second largest ones) second; medium-sized seeds (*Q. serrata* and *C. glauca*) and smallest seeds (*C. fargesii*) had a highly concentrated distribution (0–5 m) near the seed stations with a shorter tail.

## 5. Dispersal distance

Mean fresh seed weight was the only significant trait in regression models explaining mean distances (forward stepwise linear regression). In each stand, mean dispersal distances of the cached seeds (primary stand, $R^2_{adj} = 0.456$, $F_{1, 14} = 11.9$, $P = 0.005$; secondary stand, $R^2_{adj} = 0.507$, $F_{1, 12} = 12.3$, $P = 0.006$) in primary caches and eaten seeds (primary stand, $R^2_{adj} = 0.643$, $F_{1, 14} = 24.4$, $P < 0.001$, secondary stand, $R^2_{adj} = 0.611$, $F_{1, 14} = 21.4$, $P = 0.001$) significantly increased with seed weight (Fig. 3).

For the seeds in primary caches (Fig. 3), mean dispersal distances were significantly different among species ($F = 13.9$, df = 4, $P < 0.001$), but not between stands ($F = 1.3$, df = 1, $P = 0.254$) or among years ($F = 0.6$, df = 2, $P = 0.563$). Two interactions in the model were significant: species*year ($F = 3.0$, df = 7, $P = 0.004$) and stand*year ($F = 3.6$, df = 2, $P = 0.028$), the other interactions were not. For the seeds eaten (Fig. 3), there were significant differences among species ($F = 54.5$, df = 4, $P < 0.001$), but not between stands ($F = 0.01$, df = 1, $P = 0.922$) and among years ($F = 2.5$, df = 2, $P = 0.086$). Nearly all the interactions in the model were significant: species*stand ($F = 3.3$, df = 4, $P = 0.01$), species*years ($F = 2.9$, df = 7, $P = 0.005$), stands*years ($F = 19.7$, df = 2, $P < 0.001$) and species*stands*years ($F = 2.0$, df = 7, $P = 0.056$). For all species, dispersal distance did not differ significantly between cached seeds and eaten seeds (all $P > 0.05$), though there were other significant relationships between stands and years, including interactions (Fig. 3).

Mean fresh seed weight was also the only significant trait in regression models explaining the maximum dispersal distance of cached seeds in the secondary stand and eaten seeds in both stands (forward stepwise linear regression). Mean dry seed weight entered into the regression model for mean dispersal distances of the cached seeds in primary stand; however, mean fresh seed weight is also significantly positive correlated with maximum dispersal distances. For either stand, maximum dispersal distances of the cached seeds (primary stand, $R^2_{adj} = 0.341$, $F_{1, 14} = 7.7$, $P = 0.017$; secondary stand, $R^2_{adj} = 0.425$, $F_{1, 12} = 10.6$, $P = 0.007$) in primary caches and eaten seeds (primary stand, $R^2_{adj} = 0.586$, $F_{1, 14} = 19.4$, $P = 0.001$, secondary stand, $R^2_{adj} = 0.429$, $F_{1, 14} = 9.3$, $P = 0.012$) also significantly increased with seed weight (Fig. 4).
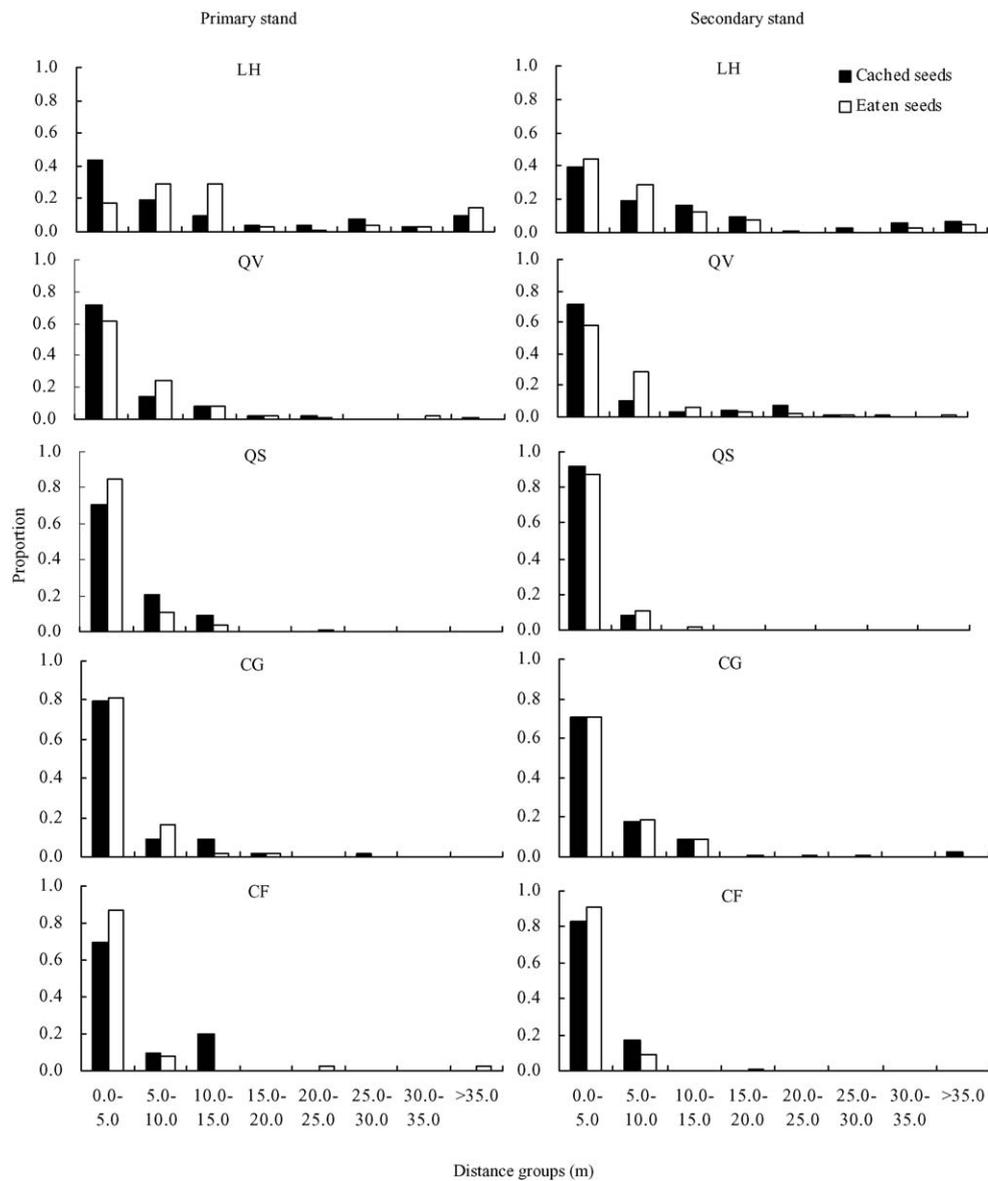
Fig. 2. Distance distributions for cached seeds (primary caches only) and eaten seeds of five fagaceous species in descending order of seed size: (LH) *L. harlandii*, (QV) *Q. variabilis*, (QS) *Q. serrata*, (CG) *C. glauca*, and (CF) *C. fargesii*. Each stand represents pooled data for 10 seeds in each of 20 cafeteria stations, in each of 3 consecutive years.

## 6. Secondary caching

A proportion of the large seeds in primary caches were found to be recovered and subsequently re-cached (i.e. *L. harlandii*, 25 secondary caches; *Q. variabilis*, 16 secondary caches), which further extended the cache distributions. Only few seeds of the medium-sized species (*Q. serrata*, no secondary caches; *C. glauca*, seven secondary caches) and small species (*C. fargesii*, no secondary caches) were re-cached. For *L. harlandii*, mean dispersal distances increased from 6.7 m for primary caches to 12.8 m for secondary caches in the secondary stand ($n = 5$), and from 17.3 to 21.9 m in the primary stand ($n = 20$). For *Q. variabilis*, mean dispersal distances increased from 6.6 m for primary caches to 8.9 m for

secondary caches in the secondary stand ($n = 4$), and from 5.0 to 9.5 m in the primary stand ($n = 12$).

## 7. Discussion

Since mean dispersal distance did not differ between the cached seeds and the eaten seeds for all species, our results indicate that the missing seeds can be excluded from consideration without biasing the interpretation of our results, though a large proportion of seeds disappeared. This suggests that the fate of seeds, i.e. eaten or cached, is independent of the distance over which small rodents move them. Therefore, we expect missing seeds and relocated seeds to have a compa-
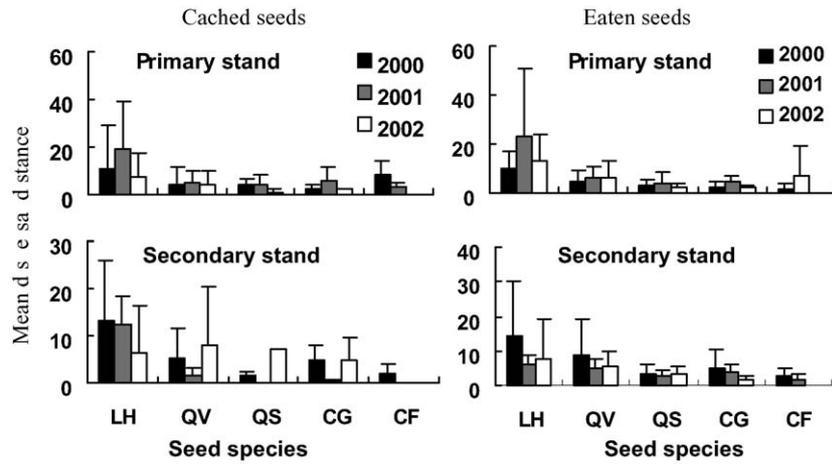
Fig. 3. Relationship between seed size and mean dispersal distance for seeds cached (primary caches only) or eaten after removal from cafeteria stations. (LH) *L. harlandii*, (QV) *Q. variabilis*, (QS) *Q. serrata*, (CG) *C. glauca*, and (CF) *C. fargesii*. Error bar indicates standard deviation (S.D.).

rable ratio of cached to eat (similar analysis in Chauvet et al., 2004).

Our results showed that dispersal distance increased with seed size whereas little variation occurred among stands and years. This confirms our hypothesis that seed size is the dominant factor to determine seed dispersal of the five fagaceous species. Greater dispersal distances for larger seeds have also been found within a tree species (e.g. Hallwachs, 1994; Jansen et al., 2002, 2004; Xiao et al., 2004a; but see Brewer, 2001; Theimer, 2003) and among different plant species (e.g. Stapanian and Smith, 1978, 1984; Hurly and Robertson, 1987; Vander Wall, 1995; Forget et al., 1998). Although Vander Wall (2003) found no consistent patterns of dispersal distance for the seeds of four *Pinus* species with different seed size, secondary dispersal by yellow pine chipmunk (*Tamias amoenus*) did increase dispersal distances to a mean of over 20 m, far beyond the distances the seeds are blown by wind. Dispersal by scatter-hoarding rodents clearly increases with both interspecific and intraspecific seed size.

Why do seed-caching rodents disperse large seeds further than small seeds? Several hypotheses exist. For example, greater food value makes larger seed size more attractive to seed-eaters according to optimal foraging theory (Stephens and Krebs, 1986); greater dispersal distances for larger seeds coincide with optimal cache spacing models (Stapanian and Smith, 1978, 1984; Clarkson et al., 1986; see also Jansen et al., 2002, 2004). Logically, larger seeds within the same species have a greater nutritional value (Grubb and Burslem, 1998). In this study, it seems reasonable to assume that seed size represents the dominant factor, because nutrient composition and caloric value are similar among these large-seeded species in the same family, though food value may be some confounded with other seed traits (e.g. tannin and seed coat). The seeds of *L. harlandii* have the largest size (4.56 g) with low tannin concentration and hard seed coat, so they are more likely to be cached by small rodents, while the seeds of *C. fargesii* are more likely to be consumed in situ due to their small size (0.46 g) and low tannin concentration (Xiao et al.,
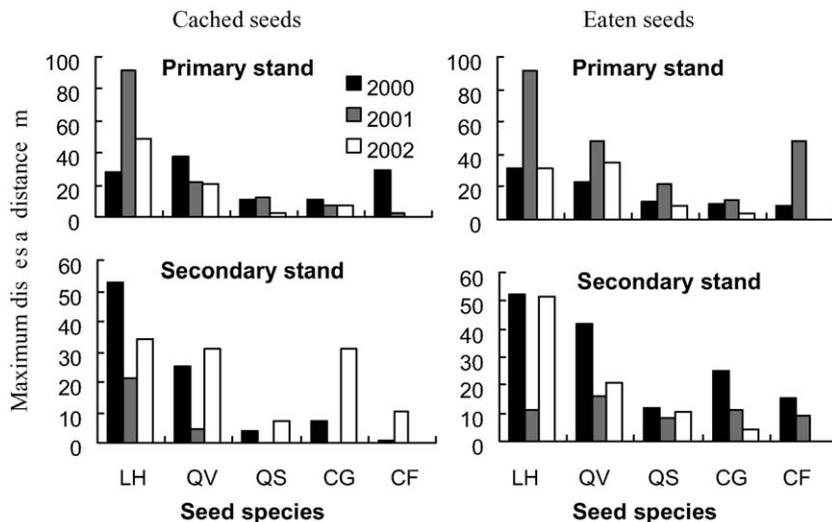


Fig. 4. Relationship between seed size and maximum dispersal distance for seeds cached (primary caches only) or eaten after removal from cafeteria stations. (LH) *L. harlandii*, (QV) *Q. variabilis*, (QS) *Q. serrata*, (CG) *C. glauca*, and (CF) *C. fargesii*.

2003a; Xiao and Zhang, 2004). The seeds of *Q. variabilis*, *Q. serrata* and *C. glauca* show little difference except mass. Our results indicate that, dispersal distances of larger seeds of *Q. variabilis* are greater than those of *Q. serrata* and *C. glauca*. In addition, higher-value seeds (e.g. larger seeds) are more likely to be cached (Smith and Reichman, 1984; Vander Wall, 1995, 2003; Jansen et al., 2002, 2004). High rates of primary caching are usually followed by high rates of cache recovery and re-caching (Jansen et al., 2004). Therefore, larger seeds (e.g. *L. harlandii* and *Q. variabilis*) facilitate increasing secondary caching, which can further reduce the relative density among caches and extend the distances or distributions from seed sources (Vander Wall and Joyner, 1998; Jansen et al., 2004; this study). On the other hand, other researchers using the similar comparative approach also found that dispersal distance was correlated with interspecific seed size, even though they had the same problem of other seed traits (e.g. Stapanian and Smith, 1978, 1984; Hurly and Robertson, 1987; Vander Wall, 1995; Forget et al., 1998; but see Vander Wall, 2003).

Since there may be strong competition for seed dispersers among co-occurring large-seeded plant species, variation in seed size and other seed traits among different tree species may shape the dispersers' behaviors (e.g. the decisions to consume or cache) to improve their own dispersal. In the same site of this study, oil tea seeds (*C. oleifera*) have high fat content (51.8%), which can increase potential food value, though the weight of oil tea seeds (0.9 g) is slightly lower than that of *Q. serrata* (0.97 g) or *C. glauca* (0.95 g). We found that the mean seed dispersal distance of oil tea (7.9 m, Xiao et al., 2004b) is not only much greater than that of *Q. serrata* and *C. glauca* (2–4 m), but also greater than that of *Q. variabilis* (4–8 m), and similar or slightly shorter than that of *L. harlandii* (mean, 6.4–19.4 m). A hard seed coat can reduce consumption in situ under or near parent trees (Zhang and Wang, 2001; Zhang et al., 2004), and higher secondary compounds (e.g. tannin) can reduce the attractiveness to seed-eaters, including rodents (Steele et al., 1993; Jansen and Forget, 2001; Xiao et al., 2003a).

If Jansen et al. (2002, 2004) provided an important counterevidence for the classic trade-off hypothesis between dispersibility and seed size within *Carapa procera* (Meliaceae), our results found that dispersal through scatter-hoarding by seed-caching rodents increases with seed size within the same family, i.e. Fagaceae. The reason for this is that the Smith–Fretwell hypothesis does not consider the potential role of secondary dispersal by seed-caching rodents or other dispersal agents (Jansen et al., 2002, 2004; Vander Wall 2003), which potentially extends the distances or ranges from parent trees (e.g. Sork, 1984; Vander Wall, 1995, 2003; Forget et al., 1998; Theimer, 2003; Zhang and Wang, 2001; Jansen, 2003; Li and Zhang, 2003; this study). Still, the Smith–Fretwell hypothesis works well for both wind-dispersed plants (e.g. Augspurger, 1986; Greene and Johnson, 1993; Benkman, 1995; Ezoe, 1998; Sakai et al., 1998) and frugivorous-bird-dispersed plants (e.g. Levey, 1987; Jordano, 1995).

There may exist an optimal seed size or size range for dispersal and scatter-hoarding by a given rodent species, since an animal can only handle seeds up to a certain size (Jansen et al., 2002; Jansen, 2003; Theimer, 2003). For example, spiny pocket mice (55 g) move only a shorter distance with larger seeds of *Astrocaryum mexicanum* (14.3 g, 61 mm length; Brewer, 2001). Since the size of both tree seeds (nuts) and seed-caching animals varies greatly in space and time, we believe that the evolution of dispersal distances may be governed by selection towards seed size by seed-caching animals in a given ecological background. For large seeds, the potential benefits from greater dispersal distances include reducing distance- or density-dependent mortality for seed predation and sib-seedling competition (Janzen, 1970, 1971; Howe and Smallwood, 1982), and increasing seed-caching and seed survival (Jansen et al., 2002, 2004; Xiao et al., 2004a), which in return increases the fitness of the large seeds.

Our conclusion findings support the idea that dispersal by seed-caching rodents may favor the evolution of large seed size in trees (Smith and Reichman, 1984), and that scatter-hoarding is advantageous for rodent-dispersed tree species. Though this study could not consider the potential effects of seed-caching birds (e.g. jays) on seed dispersal of large-seeded species, these animals might have the potential to change the spatial patterns caused by seed-caching rodents, which mainly determine local spatial patterns of large-seeded species (Den Ouden et al., 2004). More studies are needed to understand the evolution of seed size and other seed traits influenced by seed-caching animals (including birds) in diverse scales of space and time, and the potential effects of this evolution on plant reproductive success.

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