

Differences of dispersal fitness of large and small acorns of Liaodong oak (*Quercus liaotungensis*) before and after seed caching by small rodents in a warm temperate forest, China

Hongmao Zhang^{a,b,c}, Yu Chen^b, Zhibin Zhang^{a,*}

^a State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, The Chinese Academy of Sciences, Beijing 100101, China

^b College of Fisheries, Huazhong Agricultural University, Wuhan 430070, China

^c Graduate School of the Chinese Academy of Sciences, Beijing 100049, China

Received 1 April 2007; received in revised form 19 September 2007; accepted 16 October 2007

Abstract

Though effect of seed size on seed fates has been widely studied, differences of dispersal fitness of large and small acorns before and after seed caching by small rodents is largely unknown. In this study, by tracking the seed fates of 2400 tin-tagged acorns (1200 large acorns with 3.2 ± 0.6 g weight, and 1200 small acorns with 0.9 ± 0.2 g weight) of Liaodong oak (*Quercus liaotungensis*) in three habitats, we compared the differences of seed consumption, removal, caching and survival between large and small acorns at four dispersal stages (at seed station, after removal, after caching and seedling recruitment) in a warm temperate forest in the Dongling Mountains, northwestern Beijing, China. This study was carried out during the period of October 2005 to May 2006. The results demonstrated that, (1) at seed stations where tagged seeds were released, large acorns had higher proportion of removal (and more quickly) and lower proportion of seed consumption by rodents than small ones; (2) after removal, large acorns were dispersed longer, and had higher proportion of seed caching than small acorns. But there was no difference in the proportions of seed consumption between large and small acorns; (3) after seed caching, large acorns had significantly lower proportions of survival than small acorns within the observed 30-days period, and the final survival proportions of initially released seeds by the next spring were very small for both large and small acorns and the difference was not significant; (4) large acorns had higher dispersal fitness before seed caching but lower dispersal fitness after seed caching than small acorns; there was no difference in total dispersal fitness between large and small acorns. In general, our findings suggest that large acorns of *Q. liaotungensis* have similar total dispersal fitness to small ones.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Small rodents; Seed size; Seed dispersal; Seed consumption; Cache survival; Seedling establishment; Fitness

1. Introduction

The interaction between plants and animals is one of the most important mechanisms in the ecology and evolution of mutualistic systems. Several studies have demonstrated that scatter-hoarding rodents, both as consumers and dispersers of seeds, play an important role in the seed-to-seedling phase of plant regeneration (e.g. Jansen et al., 2004; Zhang et al., 2005; Theimer, 2005). Many factors, such as seed characteristics and environmental factors, may affect seed hoarding behavior of rodents (Li and Zhang, 2003; Lu and Zhang, 2004), and

subsequent seedling recruitment (Duncan and Chapman, 1999; Li and Zhang, 2003).

The nutritional quality of plant seeds and fruits is an important factor affecting seed-eating vertebrates' decisions to forage and cache (Vander Wall, 1990). Janzen (1971) suggested that large seeds (heavier and larger) might experience a lower probability of survival due to higher predation before dispersal and higher discovery and pilferage after being cached (also see Clarkson et al., 1986). However, Jansen et al. (2002) demonstrated that large seeds were dispersed further distances from parent trees, and then they suffered from smaller pilfering and rediscovering. The higher-quality caching of large seeds can subsequently translate into a greater probability of large seeds escaping consumption (Jansen et al., 2002, 2004) and subsequently germinating to the seedling stage (Jansen, 2003).

* Corresponding author. Tel.: +86 10 6480 7213; fax: +86 10 6480 7099.

E-mail address: zhangzb@ioz.ac.cn (Z. Zhang).

Large seeds may have higher probability for seedling establishment (Harper et al., 1970; Stanton, 1984, 1985; Leishman et al., 2000). Several studies have indicated that large seeds were more likely selected by rodents for their abundant nutrition (e.g. Vander Wall, 1995; Forget et al., 1998; Jansen and Forget, 2001; Jansen et al., 2004; Xiao et al., 2004a), and dispersal distance increases with seed size (e.g. Jansen et al., 2002; Xiao et al., 2004a; but see Brewer, 2001). Unfortunately, most of these studies did not compare the difference of seed survival after caching between large and small seeds, and thus the total effect of seed size on dispersal fitness (survival of scatter-hoarded or cached seeds) of large or small seeds is largely unknown. Previous studies showed that low-quality seeds suffered higher consumption *in situ* (e.g. Xiao et al., 2004b), and large cache suffered higher losses (Zhang and Zhang, 2006). These observations suggest that seed dispersal fitness of large or small seeds may differ before and after seed caching.

Liaodong oak (*Quercus liaotungensis*) is one of the common climax tree species in warm temperate broad-leaved deciduous forest in north China (Chen, 1992). Fresh acorn of *Q. liaotungensis* is ovoid, 13.3 ± 2.1 mm width, 17.8 ± 2.7 mm length and 2.0 ± 0.9 g weight ($n = 50$). Acorns of *Q. liaotungensis* mature and fall during the last 10 days of August to the end of September, and become seedlings next spring. Due to the high predation by small rodents, the natural seeding regeneration rate of *Q. liaotungensis* is very low ($<0.1\%$), even in the acorn mast-years (Li and Zhang, 2003, 2007).

The purpose of this study aims to compare differences of seed consumption, removal, scatter-hoarding and survival between large and small acorns of *Q. liaotungensis* at four dispersal stages (at seed stations, after removal, after caching and seedling recruitment). We want to test the two opposite hypothesis: (1) large acorns have lower predation and higher survival or seedling establishment (Jansen et al., 2002); and (2) large acorns have higher predation and lower survival or seedling establishment (Janzen, 1971). We also want to test our hypothesis that large acorns have higher dispersal fitness before seed caching but lower dispersal fitness after seed caching than small ones. Our hypothesis is based on the assumption that large acorns with high nutrition values are more likely cached by rodents for future consumption, but large acorns with large smell are more likely pilfered or re-discovered by rodents. Because only scatter-hoarding seeds benefit seedling recruitment, we define the survival proportion of scatter-hoarded (cached) seeds as the seed dispersal fitness in this study.

2. Methods

2.1. Study site

We carried out the study in a hill nearby the Liyuanling village ($40^{\circ}00'N$, $115^{\circ}30'E$, 1140 m ASL), Mentougou district, Beijing, China, in the Dongling Mountains with a temperate continental monsoon climate. Shrublands, secondary forests and abandoned farmlands are main types of vegetations. The area had been heavily disturbed by human activities in the last several decades.

Q. liaotungensis, wild walnut (*Juglans mandshurica*), wild apricot (*Prunus armeniaca*) and larch (*Larix principis-rupprechtii*) are the predominant tree species, with some Chinese pine (*Pinus tabulaeformis*) and cultivated walnut (*Juglans regia*) trees occurring sparsely throughout the region. Forests of *Q. liaotungensis* are a typical vegetation type in the study site. Due to extensive cutting by local residents, only small patches of secondary grown oaks remain among scattered shrublands (Sun et al., 2004). Detailed information about the study site has been described in our several previous publications (e.g. Li and Zhang, 2003, 2007; Lu and Zhang, 2004, 2005).

2.2. Experimental plots

We selected three areas of about 3.0 ha each in shrubland, secondary forestland and abandoned farmland, respectively as experimental plots. The dominant plant species in the shrubland plot include young trees of *Q. liaotungensis* and elm (*Ulmus laciniata*) with 2.2 ± 1.7 m ($n = 100$) tall and 65% total cover. This shrubland plot is located in a southeastern-facing slope of $30\text{--}45^{\circ}$. *Q. liaotungensis* and *L. principis-rupprechtii* are the dominant plant species with 8.2 ± 3.2 m ($n = 100$) tall and nearly 100% cover in the secondary forest plot. Except for some grass and shrubs, most part is leaf litters or bare ground underneath the canopy. The secondary forest plot is located in a northeastern-facing slope of $45\text{--}65^{\circ}$. *Artemisia* Linn spp., *Elymus excelsus*, *Poa* spp. and *Dendranthema* (DC.) Des Moul. spp. are dominant grass plants with 0.9 ± 0.5 m tall and $>80\%$ cover in the abandoned farmland plot, and some *J. regia* and *P. armeniaca* trees sparsely distributed in it. This farmland plot is located in a southeastern-facing slope of $40\text{--}55^{\circ}$.

Within each experimental plot there was a transect about 300 m long along the slope. Previous study indicated that most acorns of *Q. liaotungensis* are dispersed within 15 m by small rodents (Li and Zhang, 2003; Lu and Zhang, 2005), we located 20 seed stations at interval of 20 m apart along each transect.

2.3. Seed marking and releasing

During seed-fall period in 2005, fresh acorns of *Q. liaotungensis* were collected in the study area. We selected intact large and small acorns for seed release according to visual size. Among them, we randomly selected 50 large and small acorns to measure the sizes and weights of them, respectively. The large acorns were 3.2 ± 0.6 g weight, 21.1 ± 1.9 mm length and 15.8 ± 1.5 mm width, while the small acorns were 0.9 ± 0.2 g weight, 14.6 ± 1.6 mm length and 10.3 ± 0.9 mm width (mean \pm S.D.). A tiny hole of about 0.5 mm width in diameter was drilled at the base of each acorn (the drilling may partially damage kernels of acorns). A small, light, uniquely coded tin-tag (3.0 cm \times 1.0 cm) was tied to each acorn with a fine steel wire (3 cm long) (Zhang and Wang, 2001; Li and Zhang, 2003, 2007; Lu and Zhang, 2005). This tin-tagged method has been shown to be more effective in tracking seed fates by small rodents than the thread-marking method because the steel wire tied to the seeds is more resistant to cutting by rodents (Xiao et al., 2006).

On October 5, 2005, by the end of seed-fall of *Q. liaotungensis*, 20 large acorns and 20 small acorns were placed on the ground surface (about 0.5 m²) of each of the 20 seed stations along the transect of shrubland plot, secondary forest plot and farmland plot. A total of 1200 large tin-tagged acorns and 1200 small tin-tagged acorns were released in this study. We checked each seed station at 09:00–13:00 every day, and recorded the status of all released seeds. The daily check was conducted until few intact acorns left at the seed stations. By following our previous studies (Zhang and Wang, 2001; Li and Zhang, 2003, 2007; Lu and Zhang, 2005), seed status at seed stations were defined as—(1) Intact *in situ* (II): tagged acorns were intact at the seed station where they are released; (2) Eaten *in situ* (EI): tagged acorns were eaten up or eaten partially, and only tin-tags left or fragments of acorns left with tin-tags at the seed station where they are released; (3) Removal (R): tagged acorns disappeared at the seed station where they are released. Let N_0 , N_{II} , N_{EI} and N_R denote the total number of tagged acorns initially released, the number of tagged seed status II, EI, and R at the seed stations, respectively. The seed removal speed is measured by the daily proportion of intact acorns *in situ* (II) at seed stations ($=N_{II}/N_0$). The proportion of eaten acorns *in situ* (EI) measures the degree of seed consumption *in situ* ($=N_{EI}/N_0$). The proportion of removed acorns (R) measures the seed dispersal by rodents ($=N_R/N_0$).

We relocated the dispersed tin-tagged acorns within 50 m around each station extensively. When a tagged acorn was located outside of the seed station where they were released, we recorded the unique code, status of acorn and distance from the seed station (dispersal distance). All primary cached acorns were re-visited at 10 days, 30 days and by next spring (May of 2006). By following our previous studies (Zhang and Wang, 2001; Li and Zhang, 2003, 2007; Lu and Zhang, 2005), the dispersed acorn status were defined as—(1) buried (B): intact tagged acorns were scatter-buried (cached) in soil or under litters with tin-tag left on the surface; (2) intact after removal (IR): intact tagged acorns laid on ground surface; (3) eaten after removal (ER): tagged acorns were eaten up with tin-tags or/and fragments of seed coat laid on ground surface; (4) missing (M): tagged acorns were not seen, more likely were moved into burrows and finally eaten (Li and Zhang, 2007). Let N_R , N_{B0} , N_{IR} , N_{ER} and N_M denote the total number of seed status R, B, IR, ER, and M, respectively. We used the total proportion of buried acorns ($=N_{B0}/N_R$) to measure caching preference of acorns by rodents after removal. We used the proportion of eaten acorns ($=N_{ER}/N_R$) to measure seed consumption after removal. The proportions of IR ($=N_{IR}/N_R$) and M ($=N_M/N_R$) acorns were calculated accordingly.

Let N_{B10} , N_{B30} , N_{BNS} denote the number of primary cached acorns survived to day 10, day 30 and next spring (May of 2006). The survivals of primary cached acorns at day 10, 30, and by next spring was measured by the proportion of survived cached acorns to the total number of primary caches ($=N_{B10}/N_{B0}$, N_{B30}/N_{B0} , N_{BNS}/N_{B0} , respectively).

The dispersal fitness before seed caching is calculated as: $F_1 = N_{B0}/N_0$. The dispersal fitness after seed caching is calculated as: $F_2 = N_{BNS}/N_{B0}$. The total dispersal fitness is calculated as: $F = F_1 \times F_2 = N_{BNS}/N_0$.

2.4. Animal trappings

On September 27–30, 2005 (just before acorn release), 40 live steel-wire traps (12 cm × 12 cm × 25 cm) baited with peanuts were placed along each of the three transects at an interval of 5 m apart to identify rodent species utilizing the habitats. The traps were checked twice each day at sunrise and sunset times. The captured animals were weighed and released immediately *in situ*. The trapping was conducted four consecutive days. The total trap-days = 40 traps × 4 days × 3 transects = 480.

2.5. Statistics and analysis

SPSS for Windows (Version 13.0) was used for conducting statistical analysis. Cox Regression was used to test differences of seed removal speeds between acorn types and among habitats. This study is a split-plot design. Generalized linear model (GLM)—univariate was used to identify effects of mainplot (three habitat plots) and subplot (acorn size) on seed fates (seed removal, seed consumption, seed caching and seed survival). Wilcoxon test was used to test the differences of seed fates between large and small acorns in each of the three habitats (mainplot). Chi-square was used to compare the differences of seed survival and dispersal fitness between large and small acorns. Because mainplots (shrubland, secondary forest and farmland) have no replicates, the habitat effect was not analyzed or discussed.

3. Results

3.1. Key rodents

A total 51 rodents of six species were captured by live traps. The dominant rodent species were *N. confucianus* (making up 41.2% of all captured animals) and *A. peninsulae* (making up 25.5%). The trap successes were little higher in shrubland

Table 1
Rodent abundances and species composition in the three experimental habitats

Habitats	<i>Niviventer confucianus</i>	<i>Apodemus peninsulae</i>	<i>Sciurotamias davidianus</i>	<i>Apodemus agrarius</i>	<i>Tscheskia triton</i>	<i>Tamias sibiricus</i>	Total	Trap success (%)
Shrubland	10	4			2	1	17	10.6
Secondary forest	4	6		2		1	13	8.1
Abandoned farmland	7	3	4	2	6		22	13.8
Total	21	13	4	4	8	2	51	
Proportion (%)	41.2	25.5	7.8	7.8	15.7	3.9		

(10.6%) and abandoned farmland (13.8%) than that in secondary forest (8.1%) (Table 1).

3.2. Seed fates at seed stations

Nearly all released acorns were eaten or removed by small rodents within 5 days after placement (Fig. 1). The seed removal speed was significantly affected by acorn size ($F = 30.827$, d.f. = 1, $P = 0.031$), not by habitat ($F = 9.013$, d.f. = 2, $P = 0.100$), and there was not significant interaction effect between acorn size and habitat ($F = 6.669$, d.f. = 2, $P = 0.513$). The removal speed of large acorns was significantly higher than that of small acorns in all habitat plots (Wald = 122.957, d.f. = 1, $P < 0.001$) (Fig. 1).

The proportion of intact seeds *in situ* (II) was significantly affected by acorn size ($F = 7.579$, d.f. = 1, $P = 0.007$), but not by habitat ($F = 1.092$, d.f. = 2, $P = 0.339$), and there was not significant interaction between acorn size and habitat ($F = 1.092$, d.f. = 2, $P = 0.339$). Larger acorns had slightly higher proportion of II than small ones in shrubland ($Z = -2.060$, $P = 0.039$), but not significant, in secondary forest ($Z = -1.732$, $P = 0.083$) and abandoned farmland ($Z = -1.890$, $P = 0.059$) (Table A.1, Fig. 2). The proportion of eaten seeds *in situ* (EI) was significantly affected by acorn size ($F = 47.308$, d.f. = 1, $P < 0.001$), but approximately by habitat ($F = 3.024$, d.f. = 2, $P = 0.053$) and interaction between acorn size and habitat was not significant ($F = 1.145$, d.f. = 2,

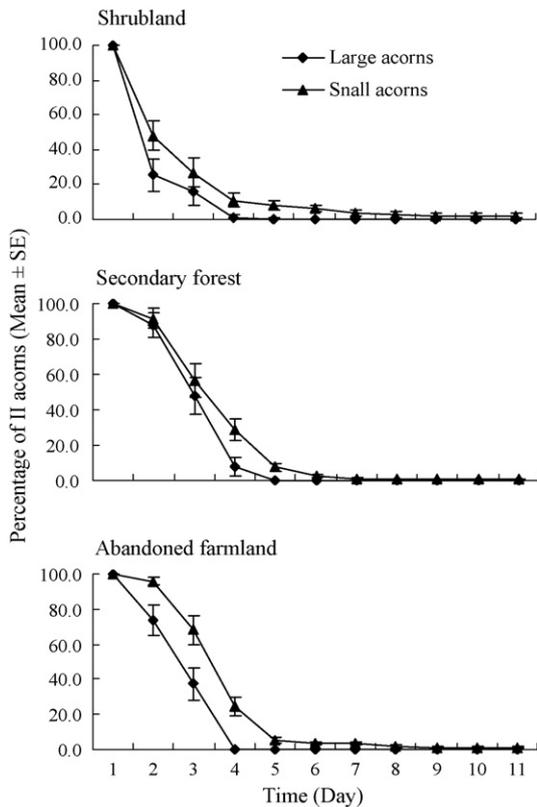


Fig. 1. Seed removal speed of large and small acorns of *Quercus liaotungensis* by small rodents at seed stations in the three habitats. The error bars are standard error. II means intact *in situ*.

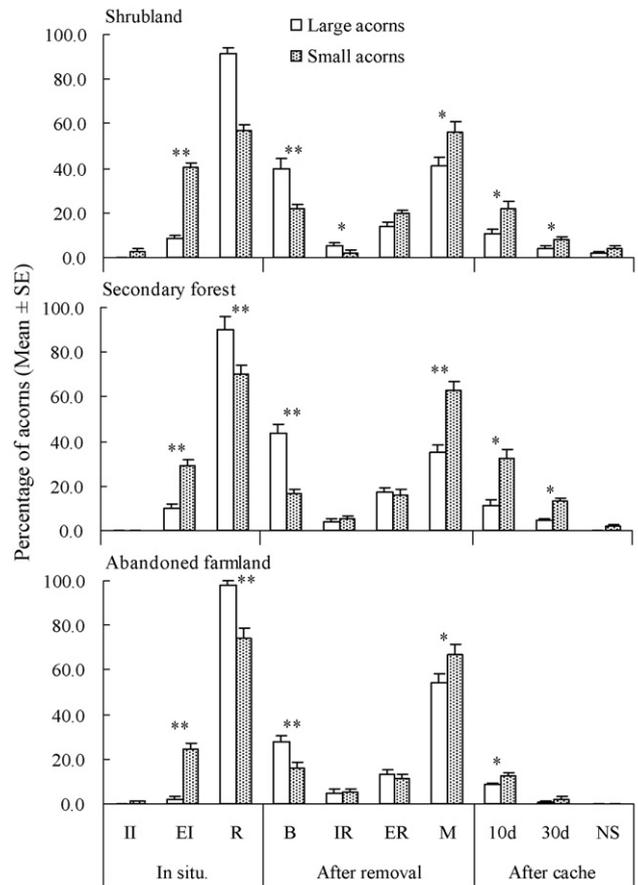


Fig. 2. Seed fates of large and small acorns of *Quercus liaotungensis* at different dispersal stages in the three habitats. Seed status include intact seeds (II), eaten seeds (EI) and removal seeds (R) at seed stations and buried seeds (B), intact seeds (IR), eaten seeds (ER) and missing seeds (M) after removal. D10, D30 and NS denote survival of cached acorns when checked at 10 days, 30 days and by next spring. The error bars are standard error. * and ** are significant marks ($*P < 0.05$ and $**P < 0.01$).

$P = 0.322$). Large acorns had significantly lower proportions of EI than small acorns in all habitat ($Z = -3.924$, $P < 0.001$ in shrubland; $Z = -3.129$, $P = 0.002$ in secondary forest; $Z = -3.833$, $P < 0.001$ in abandoned farmland) (Table A.1, Fig. 2). The proportion of removal seeds (R) was significantly affected by both acorn size ($F = 55.052$, d.f. = 1, $P < 0.001$) and habitat ($F = 3.545$, d.f. = 2, $P = 0.032$), but interaction between acorn size and habitat was not significant ($F = 1.092$, d.f. = 2, $P = 0.339$). Large acorns had significantly higher proportion of R in shrubland ($Z = -3.520$, $P < 0.001$), in secondary forest ($Z = -3.744$, $P < 0.001$) and in abandoned farmland ($Z = -3.833$, $P < 0.001$) (Table A.1, Fig. 2).

3.3. Seed fates after removal

The proportion of buried seeds (B) was significantly affected by acorn size ($F = 44.917$, d.f. = 1, $P < 0.001$) and habitat ($F = 3.714$, d.f. = 2, $P = 0.027$), but the interaction between acorn size and habitat was not significant ($F = 1.837$, d.f. = 2, $P = 0.164$). Large acorns had significantly higher proportion of B than small acorns in shrubland ($Z = -2.857$, $P = 0.004$), in

secondary forest ($Z = -3.398$, $P = 0.001$); and in abandoned farmland ($Z = -2.696$, $P = 0.007$) (Table A.1, Fig. 2). The proportions of both intact seeds (IR), and eaten seeds (ER) were not significantly affected by acorn size (for IR, $F = 0.523$, d.f. = 1, $P = 0.471$; for ER, $F = 0.234$, d.f. = 1, $P = 0.629$) and habitat (for IR, $F = 0.959$, d.f. = 2, $P = 0.386$; for ER, $F = 1.650$, d.f. = 2, $P = 0.197$), and interaction between acorn size and habitat was also not significant for IR ($F = 2.441$, d.f. = 2, $P = 0.092$) and for ER ($F = 1.804$, d.f. = 2, $P = 0.169$). There was no significant differences between large and small acorns in the proportion of IR ($Z = -1.020$, $P = 0.308$ for shrubland; $Z = -0.797$, $P = 0.426$ for secondary forest; $Z = -0.466$, $P = 0.641$ for abandoned farmland) and no significant differences in proportions of ER ($Z = -1.850$, $P = 0.064$ for shrubland; $Z = -0.382$, $P = 0.702$ for secondary forest; $Z = -0.503$, $P = 0.615$ for abandoned farmland) (Table A.1, Fig. 2). The proportion of missing seeds (M) was significantly affected by acorn size ($F = 35.019$, d.f. = 1, $P < 0.001$) and habitat ($F = 6.516$, d.f. = 2, $P = 0.002$), but interaction between acorn size and habitat was not significant ($F = 1.739$, d.f. = 2, $P = 0.180$). Small acorns had higher proportion of M than large ones in all habitats ($Z = -2.330$, $P = 0.020$ in shrubland; $Z = -3.360$, $P = 0.001$ in secondary forest; $Z = -2.277$, $P = 0.023$ in abandoned farmland). (Table A.1, Fig. 2).

3.4. Survival of cached acorns

The survival proportion of cached acorns at 10 days was significantly affected by acorn size ($F = 6.581$, d.f. = 1, $P = 0.012$), but not by habitat ($F = 0.227$, d.f. = 2, $P = 0.797$) and the interaction between acorn size and habitat was not significant ($F = 0.737$, d.f. = 2, $P = 0.481$). Small cached acorns had significantly higher proportions of survival at 10 days than large acorns in all habitats ($\chi^2 = 78.449$, d.f. = 1, $P < 0.001$ in shrubland; $\chi^2 = 63.639$, d.f. = 1, $P < 0.001$ in secondary forest and $\chi^2 = 4.463$, d.f. = 1, $P = 0.035$ in abandoned farmland). The survival proportions of cached acorns at 30 days were not significantly affected by acorn size ($F = 3.039$, d.f. = 1, $P = 0.085$) and habitat ($F = 1.481$, d.f. = 2, $P = 0.233$), and there was not significant interaction between acorn size and habitat ($F = 1.130$, d.f. = 2, $P = 0.327$) (Fig. 2). Caches of small acorns had significant higher proportion of survival at 30 days in shrubland ($\chi^2 = 98.061$, d.f. = 1, $P < 0.001$) and secondary forest ($\chi^2 = 11.488$, d.f. = 1, $P = 0.001$) than small acorns, but this difference was not significant in abandoned farmland ($\chi^2 = 1.103$, d.f. = 1, $P = 0.294$). The survival proportions of cached acorns at the next spring was not significantly affected by acorn size ($F = 2.057$, d.f. = 1, $P = 0.155$) and habitat ($F = 1.119$, d.f. = 2, $P = 0.331$), and interaction between acorn size and habitat was not significant ($F = 0.620$, d.f. = 2, $P = 0.540$) (Fig. 2). Only three large acorns, two small acorns in shrubland and one small acorn in secondary forest survived to the next spring.

3.5. Dispersal fitness and seedling establishment

The dispersal fitness (F_1) before seed caching of large acorns (0.3433) was significantly larger than that of small ones

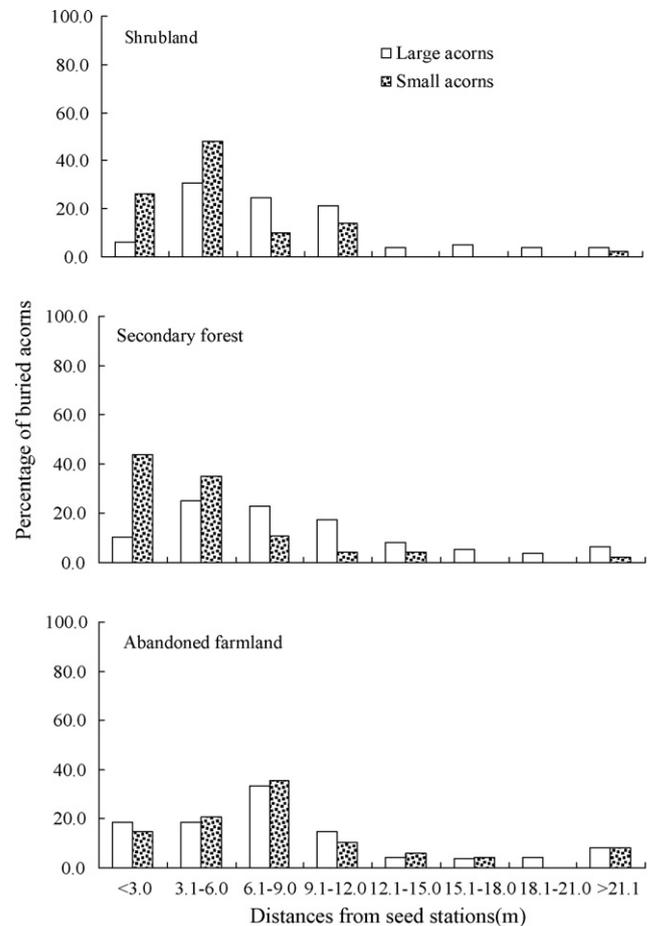


Fig. 3. Dispersal distances of cached acorns of *Quercus liaotungensis* in the three habitats.

(0.1200) ($\chi^2 = 35.110$, d.f. = 1, $P < 0.001$). The dispersal fitness after dispersal (F_2) of large acorns (0.0073) was significantly smaller than that of small ones (0.0208) ($\chi^2 = 53.210$, d.f. = 1, $P < 0.001$). There were no differences in total dispersal fitness (F) between large acorns (0.0025) and small acorns (0.0025). Of the 2400 released acorns, none of them produced seedlings by the next spring (Table A.1).

3.6. Dispersal distances

Most of the acorns were dispersed less than 15 m in all habitats (Fig. 3). The mean dispersal distance significantly affected by acorn size ($F = 21.429$, d.f. = 1, $P = 0.043$) and habitat ($F = 19.639$, d.f. = 2, $P = 0.046$), the interaction between acorn size and habitat was not significant ($F = 1.957$, d.f. = 2, $P = 0.142$). Large acorns had significantly longer dispersal distances than small acorns in all habitats ($Z = -4.026$, $P < 0.001$ in shrubland, $Z = -3.741$, $P < 0.001$ in secondary forest and $Z = -4.019$, $P < 0.001$ in abandoned farmland) (Table 2, Fig. 3).

4. Discussions

Our study revealed a different pattern of dispersal fitness for both large and small acorns of *Q. liaotungensis*. Large acorns

Table 2
Mean dispersal distances of the buried acorns of *Quercus liaotungensis* by small rodents

Habitats	Acorn types						Wilcoxon	
	Large acorns			Small acorns			Z	P
	N	Mean ± S.D. (m)	Range (m)	N	Mean ± S.D. (m)	Range (m)		
Shrubland	146	9.72 ± 0.82	0.4–60.0	50	5.06 ± 0.73	0.4–30.0	−4.026	<0.001
Secondary forest	158	9.11 ± 0.66	0.3–50.5	46	3.99 ± 0.78	0.4–23.8	−3.741	<0.001
Abandoned farmland	108	10.79 ± 0.80	0.8–40.0	48	7.80 ± 0.79	0.7–38.5	−4.019	<0.001

had better dispersal fitness before seed caching but worse dispersal fitness after seed caching. The total dispersal fitness was not different between large and small acorns. Our results support the Janzen's (1971) hypothesis in one part that large seeds have a lower probability of survival after being cached, but not the other part that large seeds may have a lower survival before dispersal. Our results obviously do not support Jansen et al.'s (2002) hypothesis that larger acorns which are dispersed further places from parent trees (or seed stations) have higher survival probability. But in our study, larger acorns were also dispersed to longer distance than small ones, which supports Jansen et al.'s (2002) hypothesis. The results support large acorns have higher dispersal fitness before seed caching but lower dispersal fitness after seed caching than small ones.

The observed pattern of seed dispersal fitness in our study could be well explained by the differences in seed caching and pilfering behavior of rodents between large and small acorns. There are many reports that low-value seeds (e.g. small acorns) are more likely eaten *in situ*, while high-value seeds (e.g. large acorns) are more likely cached by rodents for future use (e.g. Vander Wall, 1990, 1995; Jansen and Forget, 2001; Xiao et al., 2004b; Caccia et al., 2006). When provided with intact and insect-infested seeds, rodents tended to eat the later and cache the former (Xiao et al., 2004b), indicating that rodents prefer to cache high nutritional seeds. Previous studies showed that large caches or large seeds are more likely re-discovered by rodents which find food heavily depend on olfaction (Zhang and Zhang, 2006, 2007; Janzen, 1971; Clarkson et al., 1986). Large cached acorns are more likely lost by pilferage, and then suffered larger predation than small ones. Our study clearly indicated that small acorns suffer very high proportion of consumption before cached. The proportion of seed consumption was not significantly different between large and small acorns after cached.

Our study also revealed that large acorns were more likely and quickly removed by small rodents. This result supports several previous studies (e.g. Steele et al., 1996; Brewer, 2001). Brewer (2001) also found the removal speeds were significantly greater for large nuts than small ones of *Astrocaryum mexicanum* by spiny pocket mouse (*Heteromys desmarestianus*). But some other studies did not find such results. Eriksson (1999) found seed removal for the seeds of *Convallaria majalis* was not related to seed size. Jansen et al. (2002) did not find any significant effect of seed size on sequence of seeds removal of *Carapa procera* by acouchies (*Myoprocta acouchy*). One possible explanation to this inconsistency is that other seed properties might be more

important than seed size in determining seed removal in the systems they studied.

We found large acorns had significant longer dispersal distances from seed stations than small acorns. This finding supports many previous observations, at both interspecific-level studies (e.g. Stapanian and Smith, 1984; Vander Wall, 1995; Forget et al., 1998; Jansen et al., 2002; Xiao et al., 2005) and intraspecific-level studies (e.g. Hurly and Robertson, 1987; Xiao et al., 2004a). For instance, both in primary and secondary stands, large seeds (1.46 ± 0.29 g) of *Q. serrata* were carried significantly further than small seeds (0.78 ± 0.15 g) from seed station by small rodents (Xiao et al., 2004a). This is generally explained by the optimal cache spacing model which predicts that scatter-hoarders hide higher value food (i.e. large acorns) in lower densities (i.e. further away) to compensate for the probability risk of pilfering (Stapanian and Smith, 1978; Clarkson et al., 1986). Very few studies do not support this model (e.g. Brewer, 2001).

By the next spring (May of 2006), of the 2400 released acorns, only 4 survived. This observation supports the previous observation that acorns of *Q. liaotungensis* suffered very high predation by rodents which has been taken as the major reason for the failure of seed regeneration of *Q. liaotungensis* forest in this region (Li and Zhang, 2003). The poor seed-fall of *Q. liaotungensis* in 2005 might also contribute the low survival of acorns. Heavy drought in spring of 2006 might be the main reason of failure of not seedling resulted from the four survived acorns.

The effect of mainplot might be complex. Because there are no replicates of the three experimental habitats, the effect of habitat type is unknown. Six rodent species (*A. peninsulae*, *A. agrarius*, *N. confucianus*, *Tscheskia triton*, *S. davidianus* and *Tamias sibiricus*) were captured in our experimental plots, a very similar result to previous studies (Wang et al., 1999; Li and Zhang, 2003; Lu and Zhang, 2005). The rodent abundance (trap success, (%)) was very similar among the three habitats but abandoned farmland seemed to have more species. It is noticeable that some other species (e.g. wild pigs, cattle, Eurasian jay and pheasant) might be involved in acorns predation of *Q. liaotungensis* (Li and Zhang, 2003), but their role might be very small in terms of their very few numbers.

Acknowledgements

Mr. Fusheng Wang, Mr. Chuigui Yi and Mr. Xianyin Shang provided helps in collecting acorns; Dr. Britta Denise Hardesty of Tropical Forest Research Centre, CSIRO and Dr. Zhishu

Table A.1

Seed fates of large and small acorns of *Quercus liaotungensis* at different dispersal stages in three experimental habitats

Habitat	Shrubland			Secondary forest			Abandoned farmland			Total	
	Large	Small	Total	Large	Small	Total	Large	Small	Total	Large	Small
Released	400 (100.0)	400 (100.0)	800 (100.0)	400 (100.0)	400 (100.0)	800 (100.0)	400 (100.0)	400 (100.0)	800 (100.0)	1200 (100.0)	1200 (100.0)
<i>In situ</i>											
Intact (II)	0 (0.0)	11 (2.8)	11 (1.4)	0 (0.0)	3 (0.1)	3 (0.4)	0 (0.0)	5 (1.2)	5 (0.6)	0 (0.0)	19 (1.6)
Eat (EI)	33 (8.3)	161 (40.3)	194 (24.3)	39 (9.8)	116 (29.0)	155 (19.4)	9 (2.3)	99 (24.8)	108 (13.5)	81 (6.8)	376 (31.3)
Removal (R)	367 (91.7)	228 (56.9)	595 (74.4)	361 (90.2)	281 (70.2)	642 (80.3)	391 (97.7)	296 (73.9)	687 (85.9)	1119 (93.2)	805 (67.1)
After removal											
Buried (B)	146 (39.8)	50 (21.9)	196 (32.9)	158 (43.8)	46 (16.4)	202 (31.5)	108 (27.6)	48 (16.2)	156 (22.7)	412 (36.8)	144 (17.9)
Intact (IR)	20 (5.4)	5 (2.2)	25 (4.2)	15 (4.2)	15 (5.3)	30 (4.7)	19 (4.9)	15 (5.1)	34 (4.9)	54 (4.8)	35 (4.3)
Eat (ER)	50 (13.6)	45 (19.7)	95 (16.0)	62 (17.2)	44 (15.7)	106 (16.5)	51 (13.0)	34 (11.5)	85 (12.4)	163 (14.6)	123 (15.3)
Missing (M)	151 (41.1)	128 (56.1)	279 (46.9)	126 (34.9)	176 (62.6)	302 (47.0)	213 (54.5)	199 (67.2)	412 (60.0)	490 (43.8)	503 (62.5)
After cache ^a											
Over 10 days	15 (10.3)	11 (22.0)	26 (13.3)	18 (11.4)	15 (32.6)	33 (16.3)	9 (8.3)	6 (12.5)	15 (9.6)	42 (10.2)	32 (22.2)
Over 30 days	6 (4.1)	4 (8.0)	10 (5.1)	7 (4.4)	6 (13.0)	13 (6.4)	1 (0.9)	1 (2.1)	2 (1.3)	14 (3.4)	11 (7.6)
Next spring ^b	3 (2.1)	2 (4.0)	5 (2.6)	0 (0.0)	1 (2.2)	1 (0.5)	0 (0.0)	0 (0.0)	0 (0.0)	3 (0.7)	3 (2.1)
Seedling ^c											
	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

Numbers in the brackets are proportions of seed status (%).

^a After cache means the number of primary buried acorns (B) which were still at their initial cache sites when checked at 10 days, 30 days and the next spring, respectively.^b Next spring means the May of 2006.^c Seedlings means survived acorns became seedlings by next spring (May, 2006).

Xiao of Institute of Zoology, CAS, provided valuable comments in improving manuscript. This work was supported by the National Natural Science Foundation of China (30430130) and Chinese Academy of Science Innovative Research International Partnership Project (CXTDS2005-4).

Appendix A

See Table A.1.

References

- Brewer, S.W., 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92, 245–255.
- Caccia, F.D., Chaneton, E.J., Kitzberger, T., 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* 113, 469–480.
- Chen, L.Z., 1992. The oak forest on north China. *Braun-Blanquetia* 8, 33–38.
- Clarkson, K., Eden, S.F., Sutherland, W.J., Houston, A.I., 1986. Density dependence and magpie food hoarding. *J. Anim. Ecol.* 55, 111–121.
- Duncan, R.S., Chapman, C.A., 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecol. Appl.* 9, 998–1008.
- Eriksson, O., 1999. Seed size variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalis*. *Acta Oecol.* 20, 61–66.
- Forget, P.M., Milleron, T., Feer, F., 1998. Patterns in post-dispersal seed removal by neotropical rodents and seed fate in relation to seed size. In: Newbery, D.M., Brown, N.D. (Eds.), *Dynamics of Tropical Communities*. Blackwell Science, Oxford, UK, pp. 25–47.
- Harper, J.L., Lovell, P.H., Moore, K.G., 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1, 327–356.
- Hurly, T.A., Robertson, R.J., 1987. Scatter-hoarding by territorial red squirrels: a test of the optimal density model. *Can. J. Zool.* 65, 1247–1252.
- Jansen, P.A., Forget, P.M., 2001. Scatter-hoarding rodents and tree regeneration. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), *Nouragues: Dynamics and Plant–Animal Interactions in a Neotropical Rainforest*. Kluwer Academic Publisher, Dordrecht, The Netherlands, pp. 275–288.
- Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J., Van Wieren, S.E., 2002. The role of seed size in dispersal by a scatterhoarding rodent. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 209–225.
- Jansen, P.A., 2003. Scatterhoarding and tree regeneration: ecology of nut dispersal in a Neotropical rainforest. Dissertation. Wageningen University, Wageningen, The Netherlands.
- 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., 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2, 465–492.
- Leishman, M.R., Wright, L.J., Moles, A.T., Westoby, M., 2000. The evolutionary ecology of seed size. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd ed. CAB International, pp. 31–59.
- Li, H.J., Zhang, Z.B., 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). *For. Ecol. Manage.* 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). *For. Ecol. Manage.* 242, 511–517.
- Lu, J.Q., Zhang, Z.B., 2004. Effects of habitat and season on removal and hoarding of seeds of wild apricot (*Prunus armeniaca*) by small rodents. *Acta Oecol.* 26, 247–254.
- Lu, J.Q., Zhang, Z.B., 2005. Effects of high and low shrubs on acorn hoarding and dispersal of Liaodong oak (*Quercus liaotungensis*) by small rodents. *Acta Zool. Sinica* 51, 195–204 (in Chinese with English abstract).
- Stanton, M.L., 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65, 1105–1112.
- Stanton, M.L., 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia* 67, 524–531.

- Stapanian, M.A., Smith, C.C., 1978. A model for seed scatter-hoarding: coevolution of fox squirrels and black walnuts. *Ecology* 59, 884–898.
- Stapanian, M.A., Smith, C.C., 1984. Density-dependent survival of scatter-hoarded nuts: an experimental approach. *Ecology* 65, 1387–1396.
- Steele, M.A., Hadj-Chikh, L.Z., Hazeltime, J., 1996. Caching and feeding decisions by *Sciurus carolinensis*: responses to weevil-infested acorns. *J. Mammal.* 77, 305–314.
- Sun, S.C., Gao, X.M., Chen, L.Z., 2004. High acorn predation prevents the regeneration of *Quercus liaotungensis* in the Dongling Mountain Region of North China. *Restor. Ecol.* 12, 335–342.
- Theimer, T.C., 2005. Rodent scatterhoarders as conditional mutualists. In: Forget, P.M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI Publishing, pp. 283–296.
- Vander Wall, S.B., 1990. *Food Hoarding in Animals*. University of Chicago Press, Chicago.
- Vander Wall, S.B., 1995. Dynamics of yellow pine chipmunk (*Tamias amoenus*) seed caches: underground traffic in bitterbrush seeds. *Écoscience* 2, 261–266.
- Wang, W., Ma, K.P., Liu, C.R., 1999. Removal and predation of *Quercus liaotungensis* acorns by animals. *Ecol. Res.* 14, 225–232.
- Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2004a. Dispersal and germination of large and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *For. Ecol. Manage.* 195, 141–150.
- Xiao, Z.S., Zhang, Z.B., Wang, Y.S., Cheng, J.R., 2004b. Acorn predation and removal of *Quercus serrata* in a shrubland in the Dujiangyan Region, China. *Acta Zool. Sinica* 50 (4), 535–540 (in Chinese with English abstract).
- Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecol.* 28, 221–229.
- Xiao, Z.S., Jansen, P.A., Zhang, Z.B., 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *For. Ecol. Manage.* 223, 18–23.
- Zhang, H.M., Zhang, Z.B., 2007. Key factors affecting the capacity of David's rock squirrels (*Sciurotamias davidianus*) to discover scatter-hoarded seeds in enclosures. *Biodivers. Sci.* 15, 329–336 (in Chinese with English abstract).
- Zhang, H.M., Zhang, Z.B., 2006. Effects of soil depth, cache spacing and cache size of sunflower (*Helianthus annuus*) seeds on seed discovery by Siberian chipmunk (*Tamias sibiricus senescens*). *Acta Theriol. Sinica* 26, 398–402 (in Chinese with English abstract).
- Zhang, Z.B., Wang, F.S., 2001. Effect of burial on acorn survival and seedling recruitment of Liaodong oak (*Quercus liaotungensis*) under rodent predation. *Acta Theriol. Sinica* 21, 35–43.
- Zhang, Z.B., Xiao, Z.S., Li, H.J., 2005. Impact of small rodents on tree seeds in temperate and subtropical forests, China. In: Forget, P.M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI Publishing, pp. 269–282.