Plant Ecol (2008) 196:135–142
DOI 10.1007/s11258-007-9340-7

Seed predation and dispersal of glabrous filbert (*Corylus Heterophylla*) and pilose filbert (*Corylus Mandshurica*) by small mammals in a temperate forest, northeast China

Xianfeng Yi · Zhibin Zhang

Received: 10 March 2007 / Accepted: 9 July 2007 / Published online: 29 July 2007

Abstract We investigated the seed dispersal of glabrous filbert (*Corylus heterophylla*) and pilose filbert (*Corylus mandshurica*), two large-seeded shrub species in a temperate forest, northeast China, September 2006. Small mammals such as *Apodemus speciosus*, *Clethrlonomys rufocanus,* and *Eutamias sibiricus*, were regarded as the main dispersal agents. More seeds were harvested by small mammals in pilose filbert (98%) than in glabrous filbert (87.5%) till our last survey. Seed removal rates differed between the two species. Fewer seeds of glabrous filbert (17.5%) were eaten in situ than pilose filbert (57.5%). More seeds of glabrous filbert were removed (70%), stay intact after removal (25.5%), eaten after removal (16%) than pilose filbert. However, more seeds were cached after removal in pilose filbert than in glabrous filbert (10.5 and 4%, respectively). Fewer tagged seeds of pilose filberts (14%) were missed than glabrous filberts (24.5%). About 8 and 12 primary caches were found in glabrous filbert and pilose filbert seeds respectively, indicating scatter hoarding. All of the removed seeds were distributed within 10 m of seed stations for both filberts. The average dispersal distances for glabrous filbert did not differ from pilose filbert. Only a small proportion of the caches remained till our last survey (2 and 1%, respectively). Based on the results, we found a difference in dispersal patterns of glabrous filbert and pilose filbert seeds. Evidences showed that glabrous filberts might be a less preferred seed species for small seed-eating mammals compared with pilose filbert, probably due to its harder and thicker husk and low seed profitability.

Keywords Seed fate · *Corylus heterophylla* · *Corylus mandshurica* Betulaceae · Northeast China

X. Yi · Z. Zhang (✉)
State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, The Chinese Academy of Sciences, Beisihuanxilu 25, Haidian District, Beijing 100080, China
e-mail: zhangzb@ioz.ac.cn

Present Address:
X. Yi
College of Agriculture, Henan University of Science and Technology, Tianjin Road 70, Jianxi District, Luoyang 471003, China
e-mail: yxfeng1975@126.com

Introduction

Animals, as to their effects, intensities and frequencies, have significant impacts on tree reproduction and are pivotal in the regeneration and demography of large-seeded trees. In particular, granivorous, seed-dispersing animals may have a large influence on early demography of trees. In natural conditions, plants often suffer heavy mortality in their seed and seedling stages due to herbivory predation (Forget

1996). Many studies have examined interactions between scatter-hoarding animals and seed-bearing plants (Price and Jenkins 1986; Vander Wall 1990 2001; Jansen and Forget 2001; Smallwood et al. 2001). In many large-seeded, seed-bearing trees, small mammals are responsible both for effective seed dispersal by their vigorous activity of seed hoarding (Vander Wall 2001), and for early-stage mortality through seed and seedling predation (Crawley 2000; Kitajima and Fenner 2000; Hulme and Benkman 2002). Plants that use the propagule to interrelate animals as dispersal agents must balance the costs of seed predation with the benefits of dispersal. Successful post-dispersal germination is a key metric that reflects these costs and benefits (Price and Jenkins 1986). However, it is not well understood how seed-bearing plants evolved to balance seed predation and seed dispersal via scatter-hoarding animals. Much attention has been paid to the dispersal biology of the oaks (Quercus, Fagaceae) (Li and Zhang 2003; Gómez 2004; Xiao et al. 2004a), apricot (*Prunus armeniaca*) (Zhang and Wang 2001), lodgepole pine (*Pinus contorta*) (Despain 2001), African mahogany (*Entandrophragma* spp.) (Medjibe and Hall 2002), oil tea (*Camellia oleifera*) (Xiao et al. 2004b), and singleleaf piñon pine (*Pinus monophylla*) (Hollander and Vander Wall 2004). However, the glabrous filbert (*Corylus heterophylla*) and pilose filbert (*Corylus mandshurica*), widely distributed shrubs in temperate forests of northeast China, are less well studied. They all produce large seeds, which may be potentially dispersed by scatter-hoarding rodents (Vander Wall 1990, 2001; Corlett 1998). Glabrous filberts and pilose filberts have a harder seed husk and lower tannin content than acorns from oaks (Xiao et al. 2003). Differences in physical and chemical seed traits play a role in determining seed predation, dispersal, and seedling establishment. So far, however, no field evidence indicates whether seed dispersal by small seed-caching mammals can lead to successful seed dispersal both for glabrous filberts and pilose filberts.

Glabrous filbert (*Corylus heterophylla*) and pilose filbert (*Corylus mandshurica*), included in the family of Betulaceae, produced large seeds with different size, mass, nutrition contents, and other traits. Glabrous filbert and pilose filbert are dominant species and make great contribution to stability and biodiversity of forest ecosystem. To evaluate different patterns of seed predation and dispersal of glabrous filbert and pilose filbert, we investigated seed dispersal by seed-caching animals by tracking individual seeds with coded tin-tags in September 2006, in a temperate broadleaved forest in the Dongfanghong Forest Center, China. Here, we address three questions: 1) Are small seed-caching mammals dispersal agents for the two filbert species? 2) How is the temporal and spatial patterns of primary and secondary seed dispersal of glabrous filbert and pilose filbert; 3) Which seed traits are closely correlated to seed dispersal by small scatter-hoarding mammals?

Materials and methods

Study site

The study was conducted in September 2006 in the Dongfanghong Forestry Center (elevation averaged at 750 m, 45° 58′ N, 129° 08′ E) in Dailing District, Yichun City, Heilongjiang Province, northeast China. The climate of experimental site is dominated by the north temperate zonal monsoon with severe and long winters and short cool summers. The annual average air temperature is 1.4°C with extremes of 35°C and −40°C. Average annual precipitation averaged at 650 mm, 80% of which falls in the short summer growing season from May to September. Vegetation is characterized by secondary broad-leaved and conifer mixing forest. In the experimental region, dominant or common canopy tree species included *Betula platyphlla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurese*, *Acer mono,* and *Tilia amurensis*, beneath the tree species, shrub such as *Corylus mandshurica*, *Corylus heterophylla*, *Fructus Schisandrae,* and *Acanthopanax senticosus* dominated. Small mammals related to seed dispersal are *Apodemus speciosus*, *Clethrlonomys rufocanus,* and *Eutamias sibiricus*. Eurasian jay, *Garrulus glandarius* is expected to be another less important species participating in large-sized seed dispersal.

Seed removal and seed fate

Since 2006 was an off year for glabrous filbert and pilose filbert seeds, we bought some of them in the market, and used water flotation to distinguish between non-infected and insect-damaged/empty seeds. Then we randomly selected 400 fresh, sound seeds and labeled them using slightly modified methods from Zhang and Wang (2001). A tiny hole 0.5 mm in diameter was drilled near the germinal disk of each seed with an electrical drill. Though the cotyledon was partly damaged, the embryo remained intact and was able to germinate, when the seeds escape post-dispersal predation by small mammals and other predators. Seeds were tied with a small, light tin-tag (length × width, 1 × 3 cm, <0.01 g) through the hole by using a thin steel wire 10 cm long, each tag being coded with a serial number to be able to identify every seed. When small mammals bury the tagged seeds in the soil, the tin-tags are often left on the surface, making them easy to be re-located. Tagging has a negligible effect on acorn removal and caching by rodents (Zhang and Wang 2001; Forget and Wenny 2005).

About 10 plots (1 × 1 m) were established as experimental seed stations for each of the two filbert species, spaced 15 m apart along a transect line. In September 2006, each plot was cleaned (without litter) to make seeds conspicuous over forest ground before spreading seeds. Then, we placed 20 tagged seeds at each seed station (each plot received only one seed species) and make them regularly spaced within plots. One day after release, we checked the tagged seeds every day at each station to investigate seed harvest and removal by small mammals, and recorded their fates. At the same time, we searched the area around each station (radius, <10 m) though daily visit with equal efforts of 10 min for two people each visit, for the tagged seeds from each station by mammals. Proximate fates of the released seeds in each plot were expressed as: intact in situ (IS), eaten in situ (EIS); eaten after removal (EAR), intact after removal (on surface) (IAR); cached after removal (in soil) (CAR); missed (may be in burrow or not seen) (M). Time to removal refers to rate of seed removal throughout a time period from the day when the seeds are released to the last survey.

When a cache was found, we carefully recorded the seed code numbers, measured the linear distance between the tagged seed found and the center of its corresponding seed station, and determined the cache location using a chopstick that was coded with the numbers of seeds. The sticks were set 20 cm away from the seed caches. In the subsequent visits, we also checked all the caches found in the first visit until the caches were removed or eaten by small mammals (this duration was defined as lifetime of caches). If a marked cache was removed, the area around the cache (radius, <10 m) was randomly searched. Primary and secondary cache sites are identified based on the coded numbers and consequent movement by small mammals. Dispersal distances are measured as the linear length from the center of released plots to the new locations of the corresponding removed seeds. Missed rates refer to the proportion of missed seeds throughout our survey.

Parameters of seed traits were also collected to test its potential correlation with seed dispersal. Seed size (cm) and mass (g) were measured with vernier caliper and electronic scale, respectively; Seed profitability was defined as the ratio of dry kernel weight to total dry seed weight. Tannin content was quantified based on folin hydroxybenzene reduction. Starch, protein, and fat contents were determined using general procedures.

Cox regression was used to compare the time to removal from seed stations between the two seed species. One-way ANOVA was used to test the difference in lifetime of caches and missed rates of tagged seeds. Independent Sample *T*-Test was used to test the difference in dispersal distances from seed stations of primary caches or eaten seeds in the two species. Differences in seed traits (size, mass, thickness, tannin content, and nutrition) were also tested using Independent Sample *T*-Test.

Results

Seed disperser identification

In the experimental site, we used wooden snare kill-traps baited with one peanut to monitor small mammal species and their numbers in the autumn (later September) in 2006. Three transects were selected and 48 trap stations were set at 5 m intervals along each transects for four consecutive nights. We determined the species and abundance of captured small mammals. In late September 2006, three small mammal species were trapped over 192 trap nights. *Apodemus speciosus* (n = 5, body mass range 20–31 g), *Clethrlonomys rufocanus* (n = 3, body mass range 22–44 g), and *Eutamias sibiricus* ($n = 1$, body mass = 82 g). We failed to capture the Eurasian jay despite they were sometimes witnessed.

Seed removal and seed fate

Our daily surveys on the two filbert seeds demonstrated that 87.5% glabrous filbert and 98% pilose filbert seeds were harvested by small mammals after placement, respectively (Figs. 1 and 2). Seed half lifetime for pilose filbert at seed stations was 9 days, however, there were 12.5% of glabrous filbert seeds remained in situ till our last survey (totally 29 days). Seed removal rates differed significantly between the two species (Wald = 6.551, $df = 1$, $P = 0.010$). Fewer seeds of glabrous filbert (17.5%) were eaten in situ than pilose filbert (57.5%). More seeds of glabrous filbert were removed (70%), stay intact after removal (25.5%), eaten after removal (16%) than pilose filbert. However, more seeds were cached after removal in pilose filbert than in glabrous filbert (10.5 and 4%, respectively). More tagged seeds (24.5%) were missed in glabrous filberts than in pilose filberts (14%) ($F = 263.834$, $df = 1$, $P = 0.000$), and their ultimate seed fates are unknown (Fig. 3).

Investigation showed all caches contained only one tagged seed of glabrous filbert or pilose filbert, indicating cache size = 1. We totally found eight primary caches in glabrous filbert seeds and 21 caches in pilose filbert seeds (Figs. 4 and 5) during our survey. For glabrous filbert, no cached seeds in primary cache sites were recovered and re-moved into new cache sites (i.e., secondary cache sites). However, some pilose filbert seeds in primary caches were re-moved or eaten in the second dispersal duration.

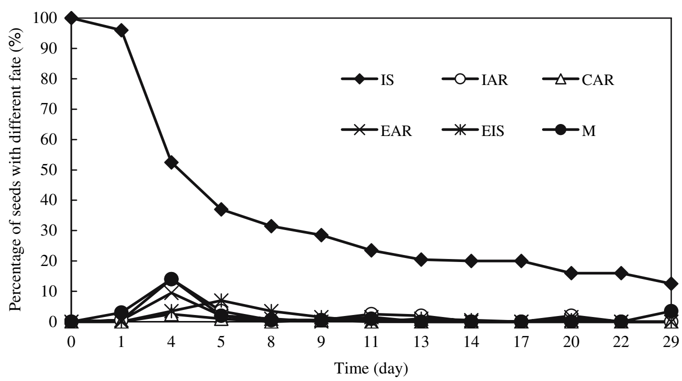
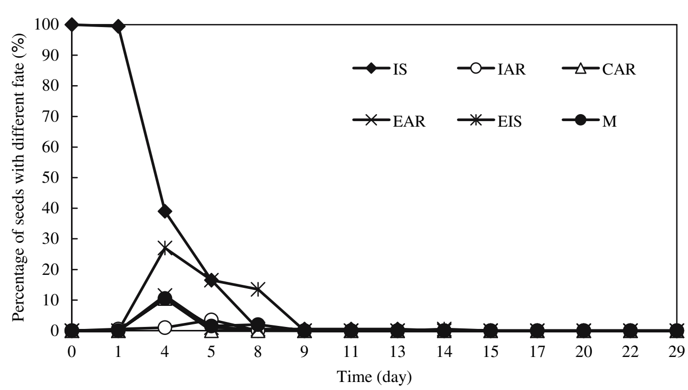


Fig. 1 Seed dynamics of *Corylus heterophylla* (Betulaceae) after placing at the released location in northeast China Note: IS, EIS, EAR, IAR, CAR, and M refer to intact in situ, eaten in situ, eaten after removal, intact after removal (on surface), cached after removal (in soil), and missed (may be in burrow or not seen), respectively. The same as in Figs. 2, 4, and 5

Fig. 2 Seed dynamics of *Corylus mandshurica* (Betulaceae) after placing at the released location in northeast China



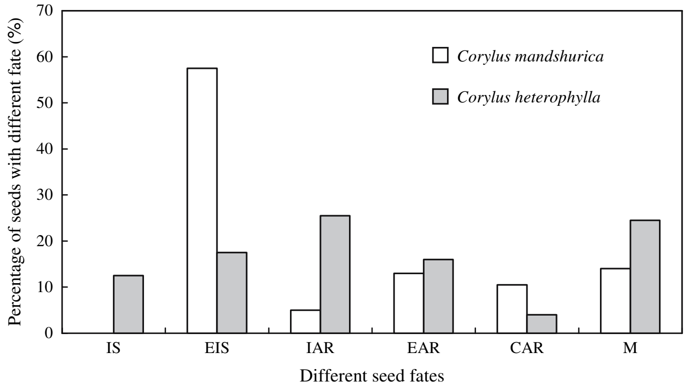


Fig. 3 Seed fates of *Corylus heterophylla* and *Corylus mandshurica* (Betulaceae) after secondary dispersal by small mammals in northeast China

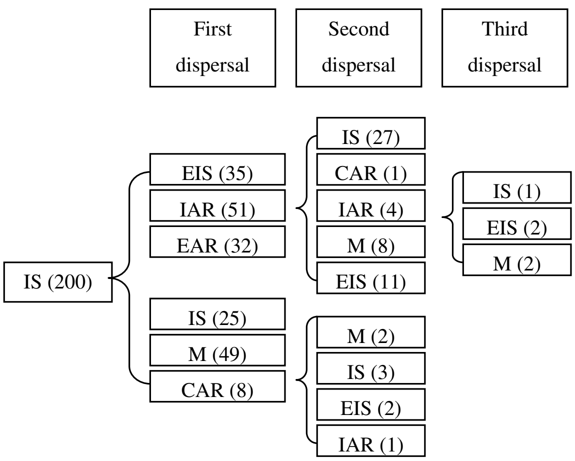


Fig. 4 Seed dispersal and following seed fates of *Corylus heterophylla* (Betulaceae) by small mammals in northeast China

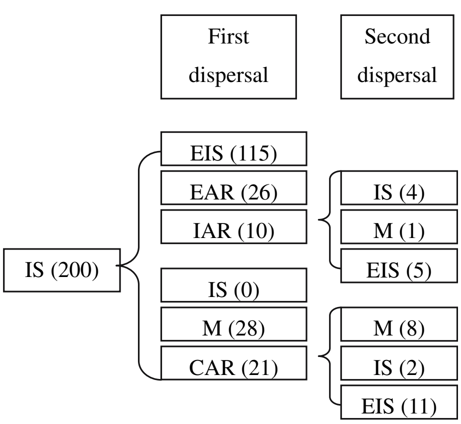


Fig. 5 Seed dispersal and following seed fates of *Corylus mandshurica* (Betulaceae) by small mammals in northeast China

Dispersal distances

All removed (including eaten after removal and intact after removal) and hoarded seeds were distributed within 10 m of seed stations for both glabrous filbert and pilose filbert (Fig. 6). The average dispersal distances were 1.83 ± 0.96 m and 1.98 ± 1.29 m for glabrous filbert and pilose filbert respectively and showed no difference (t = 0.585, df = 146, P = 0.559). The maximum dispersal distance for glabrous filbert and pilose filbert reached 8.0 m and 8.7 m, respectively.

Secondary dispersal and cache survival

Although second dispersal occurred, we failed to find re-cached seeds in glabrous filbert and pilose filbert. Among primary caches in glabrous filbert and pilose filbert, three and two cached seeds remained till our last survey (29 days). Mean lifetime of primary caches for the two filbert seeds were 12.57 ± 8.37 and 11.77 ± 9.79 days respectively and showed no difference (F = 1.855, df = 1, P = 0.266), therefore, only a small proportion of the caches remained till our last survey (1.5 and 1% for glabrous filbert and pilose filbert, respectively).

Differences between seed traits of glabrous filbert and pilose filbert

As mentioned in Table 1, seeds of glabrous filberts (1.58 × 1.44 cm) have a larger size in length and width than pilose filbert (1.43 × 1.20 cm) (t = 2.752, df = 22, P = 0.012; t = 7.084, df = 22, P = 0.000). A harder husk of 0.24 ± 0.03 cm thick measured in

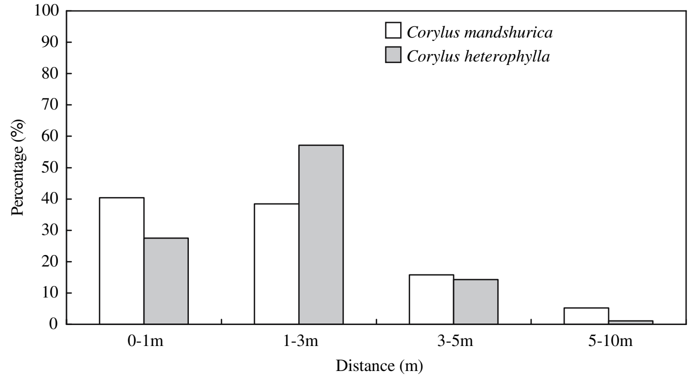


Fig. 6 Frequency distributions of dispersal distances of *Corylus heterophylla* and *Corylus mandshurica* (Betulaceae) from seed released stations in northeast China

glabrous filberts seeds than in pilose filbert of 0.11 ± 0.01 cm ($t = 9.468$, $df = 19$, $P = 0.000$). Although glabrous filberts have large seed size with a greater nutritional value (Table 1), showed lower dry seed profitability (kernel weight/seed weight, %) of 18.66% than pilose filbert (38.57%, two time as glabrous filbert) ($t = -9.290$, $df = 44$, $P = 0.000$) (Table 1).

Discussion

Seed predation and dispersal by small seed-caching mammals

Our results indicated that small seed-caching mammals act as potential seed dispersers in glabrous filberts and pilose filberts. Nevertheless, glabrous filbert seemed to be less preferred food sources for small mammals compared with pilose filbert, as indicated by the following three facts: 1) lower eaten rate (41%) and relatively long half seed lifetime (5–8 days) at seed released locations; 2) low caching rate, only 1.5% the re-located seeds were cached; 3) high proportion of seeds (including re-located removed seeds) remained intact in situ (25.5%) till our last survey. However, we witnessed an opposite fact in pilose filbert in this study: higher eaten rate (57.5%) and relatively shorter half seed lifetime (3–4 days) at seed released locations; relatively higher caching rate (10.5%) and, lower proportion of seeds remained on the ground (2%) till our last survey.

Compared with pilose filbert, glabrous filbert seed with a hard seed husk potentially increases seed handling time for seed-eating animals and thus increases the seed-eaters risk of predation (Jacobs 1992; Hadj-Chikh et al. 1996). Therefore, small seed-caching mammals may reduce instant consumption (Zhang and Wang 2001; Li 2002; Zhang et al. 2005). These facts may strengthen our above explanation

Table 1 Seed traits of *Corylus heterophylla* and *Corylus mandshurica* collected from northeast China

Seed traits	Seed species	
	Corylus mandshurica	*Corylus heterophylla*
Seed rain duration	September	September
Size (cm × cm)	1.43 × 1.20 ($n = 12$)	1.58 × 1.44 ($n = 12$)
Mass (g)	0.73 ± 0.08 ($n = 12$)	1.18 ± 0.28 ($n = 12$)
Thickness of seed husk (cm)	0.11 ± 0.01 ($n = 10$)	0.24 ± 0.03 ($n = 11$)
Seed profitability (kernel weight/total seed weight) (%)	38.57 ± 3.55 ($n = 24$)	18.66 ± 4.29 ($n = 22$)
Tannin (%)	3.7	2.6
Fat (%)	55.2	62.1
Protein (%)	15.4	17.4
Starch (%)	8.26	15.8

why small mammals spent fewer efforts depositing glabrous filberts than pilose filbert. Hardness of husk and structures might play an important role in determining the dispersal patterns of the two different filberts.

For cache size, all re-located caches contained only one tagged seed (i.e., cache size = 1) both for glabrous filbert and pilose filbert, suggesting scattering-caching of the two different filberts by small mammals. Scattering-caching is considered to be related to large size and mass of seeds (Jansen et al. 2004). High proportion of one-seed caches indicates lower risk of predation and pilferage, lower sibling competition and more potential sites for seedling establishment (Forget 1996). The results also suggested no larder-hoarding in the two filbert species. Despite no difference found in mean dispersal distances, missed rate of tagged seeds are higher in glabrous filbert than in pilose filbert. According to the optimal cache spacing models, large seeds are cached further than small ones (Stapanian and Smith 1978; Clarkson et al. 1986). Some tagged seeds of glabrous filbert might have been transported into further locations beyond our observation, due to its larger size in length and width than pilose filbert.

Seed traits of filberts related to small mammal dispersal

Our results demonstrated that glabrous filbert was, unlike pilose filbert, a less preferred seed species for small rodents and/or other animals in the experimental site. Some defensive traits might account for this fact, e.g., secondary compounds and seed coat (Zhang et al. 2005). A harder husk of 0.24 ± 0.03 cm thick measured in glabrous filberts seeds, which potentially increases seed handling time for seed-eating animals and thus increases the seed-eaters risk of predation compared with pilose filbert (Jacobs 1992; Hadj-Chikh et al. 1996). Although glabrous filberts have large seed size with a greater nutritional value (Table 1), lower dry seed profitability (kernel weight/seed weight) (%) averaged at 18.66%, might lose attractiveness to small mammals. However, a thin husk measured in pilose filberts seeds, which potentially decreases seed handling time for seed-eating animals and thus lower the seed-eaters risk of predation (Jacobs 1992; Hadj-Chikh et al. 1996). In fact, pilose filberts have a relatively small seed with a greater nutritional value (Table 1), dry seed profitability (kernel weight/seed weight) averaged at 38.57% (two time as glabrous filbert) (Table 1), making themselves more attractive and effective to predation of small mammals. It is possible that a thin husk and higher seed profitability, together with large size/mass and high nutrient levels might strengthen high harvesting rate of pilose filberts, rather than glabrous filberts. Our data showed that glabrous filbert might be a less preferred seed species for small seed-eating mammals compared with pilose filbert, as indicated by the lower proportion of seeds eaten in situ and after removal.

Our previous studies are focused on seed dispersal and seed fate of oaks (Fagaceae) (Li and Zhang 2003; Xiao et al. 2004a; Xiao and Zhang 2006, Xiao et al. 2006; Xiao et al. 2007), apricot (Zhang and Wang 2001), and oil tea (Xiao et al. 2004b; Xiao and Zhang 2006) in southwest and north China. Despite these studies observed higher proportion of cached seeds and successful seedling establishment, we witnessed an extremely low level of cached seeds either for glabrous filbert and pilose filbert in northeast China. However, in natural condition they act as dominant species and cluster in a great number under layer of canopy (personal field observation, 2006). Glabrous filbert and pilose filbert are fond of solar radiation and their reproduction is strongly light-dependent, as revealed from the fact that most mature filberts are unable to produce adequate seeds beneath the dense canopy. The lower level of cached seeds by small mammals and higher biomass of filberts may generate a paradox. However, we have little knowledge of if there is a clone reproduction through root ramet of the two filbert species and consequently offset the contribution of small mammals. Therefore, the dispersal and reproduction of the two filberts should be further investigated as lower cached rates of filbert seeds were obtained in this study.

Acknowledgments We are very grateful to two anonymous researchers for their critical comments to this article. We also thank the Dongfanghong Forestry Center for support. Funds were provided by the key project of National Natural Science of China (30430130), the key program of the Ministry of Science and Technology (G2000046802) and the Innovation Programs of Chinese Academy of Sciences (KSCX2-SW-105 and KSCX2-SW-103) and K. C. Wong Education Foundation, Hong Kong.

References

Clarkson K, Eden SF, Sutherland WJ (1986) Density dependence and magpie food hoarding. J Anim Ecol 55:111–121

Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the oriental (*Indomalayan*). Regional Biol Rev 73:413–448

Crawley MJ (2000) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International Publishing, Wallingford, pp 167–182

Despain DG (2001) Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. Forest Ecol Manage 141:59–68

Forget PM (1996) Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rain forest in French Guiana. J Trop Ecol 12:751–761

Forget PM, Wenny D (2005) How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal. In: Forget PM, Lambert J, Hulme PE, Vander Wall SB (eds) Seed fate: seed predation, seed dispersal and seedling establishment. CABI, Publishing, Wallingford, pp 379–393

Gómez JM (2004) Bigger is not always better: conflicting selective pressures on seed size in *Quercus Ilex*. Evolution 58:71–80

Hadj-Chikh LZ, Steele MA, Smallwood PD (1996) Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. Anim Behav 52:941–948

Hollander JL, Vander Wall SB (2004) Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). Oecologia 138:57–65

Hulme PE, Benkman CW (2002) Granivory. In: Herrera CM, Pellmyr O (eds) Plant-animal interactions. Blackwell Science, Oxford, pp 132–154

Jacobs LF (1992) The effect of handling time on the decision to cache by grey squirrels. Anim Behav 43:522–524

Jansen PA, Forget PM (2001) Scatter-hoarding rodents and tree regeneration. In: Bongers F, Charles-Dominique P, Forget PM, Théry M (eds) Nouragues: dynamics and plant-animal interactions in a neotropical rainforest. Kluwer Academic Publisher, Dordrecht, the Netherlands, pp 275–288

Jansen PA, Hemerik L, Bongers F (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecol Monogr 74:569–589

Kitajima K, Fenner M (2000) Ecology of seedling regeneration. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International Publishing, Wallingford, pp 331–359

Li HJ (2002) Effect of small rodents on seed regeneration of forest. Ph.D. thesis. Institute of Zoology, Chinese Academy of Sciences, Beijing (in Chinese with English abstract)

Li HJ, Zhang ZB (2003) Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). Forest Ecol Manage 176:387–396

Medjibe V, Hall JS (2002) Seed dispersal and its implication for silvicuture of African mahogany (*Entandrophragma spp.*) in undisturbed forest in the Central African Republic. Forest Ecol Manage 170:249–257

Price MV, Jenkins SH (1986) Rodents as seed consumers and dispersers. In: Murray DR (eds) Seed dispersal. Academic Press, Sydney, Australia, pp 191–235

Smallwood PD, Steele MA, Faeth SH (2001) The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: tannins, insects, and seed germination. Amer Zool 41:840–851

Stapanian MA, Smith CC (1978) A model for seed scatter-hoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884–898

Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press

Vander Wall SB (2001) The evolutionary ecology of nut dispersal. Bot Rev 67:74–117

Xiao ZS, Zhang ZB, Wang YS (2003) Observations on tree seed selection and caching by Edward's long-tailed rats (*Leopoldamys edwardsi*). Acta Theriol Sin 23:208–213 (in Chinese with English summary)

Xiao ZS, Zhang ZB, Wang YS (2004a) Dispersal and germination of big and small nuts of *Quercus serrata* in subtropical evergreen broadleaved forest. Forest Ecol Manage 195:141–150

Xiao ZS, Zhang ZB, Wang YS (2004b) Impacts of scatter-hoarding rodents on restoration of oil tea *Camellia oleifera* in a fragmented forest. Forest Ecol Manage 196:405–412

Xiao ZS, Zhang ZB (2006) Nut predation and dispersal of Harland Tanoak *Lithocarpus harlandii* by scatter-hoarding rodents. Acta Oecologica 29:205–213

Xiao ZS, Jansen PA, Zhang ZB (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. Forest Ecol Manage 223:18–23

Xiao ZS, Harris M, Zhang ZB (2007) Acorn defenses to herbivory from insects: implications for the joint evolution of resistance, tolerance and escape. Forest Ecol Manage 238:302–308

Zhang ZB, Wang FS (2001) Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). Acta Ecol Sin 21:839–845

Zhang ZB, Xiao ZS, Li HJ (2005) Impact of small rodents on tree seeds in temperate and subtropical forests, China. In: Forget PM, Lambert J, Hulme PE, Vander Wall SB (eds) Seed fate: seed predation, seed dispersal and seedling establishment. CABI, Publishing, Wallingford, pp 269–282