



Impacts of scatter-hoarding rodents on restoration of oil tea *Camellia oleifera* in a fragmented forest

Zhishu Xiao, Zhibin Zhang*, Yushan Wang

State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology,
Chinese Academy of Sciences, Beisihuanxilu 25, Haidian District, Beijing 100080, China

Received 15 December 2003; received in revised form 24 March 2004; accepted 4 April 2004

Abstract

Few studies have evaluated the role of seed dispersal by animals (especially scatter-hoarding rodents) in natural restoration in fragmented forests. In order to assess the potential benefits of oil tea from natural dispersal by seed-caching rodents, we tracked the individual seeds with coded tin tags of oil tea *Camellia oleifera* (Theaceae), an economically important evergreen shrubs, by establishing artificial seed sources (mimicking natural seed rain) in a secondary stand (i.e. *Camellia*-poor stand, where no oil tea shrubs grow) in a fragmented forest in the Dujiangyan Region of Sichuan Province, China. Our results indicate that the total survival of the released seeds was zero, which confirms the hypothesis that poor seeding regeneration may be caused by poor seed sources and subsequent high rodent predation in fragmented secondary forests. As small rodents repeatedly handled the tagged seeds, the proportions of seed consumption (i.e. eaten) and removal were constant in both Dispersal I and Dispersal II, but the caching proportion significantly decreased and the missing proportion significantly increased. Our results also indicate that seed-caching rodents are important in promoting natural regeneration of oil tea through scatter-hoarding seeds in soil: (1) seed removal was high (91.2%); (2) many removed seeds were found to be cached (48.2% for the relocated seeds); (3) dispersal distances of the cached seeds ranged from 0 to 38 m (mean, 7.9 m); (4) 81.3% of the caches (including primary and secondary caches) contained only one seed. Therefore, seed-caching rodents could have the potential to help restore natural populations of oil tea if we increase oil tea seed sources in the *Camellia*-poor stands.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Forest fragmentation; Restoration; Natural seed dispersal; Seed-caching rodents; Oil tea *Camellia oleifera*; Dujiangyan region; China

1. Introduction

Forest fragmentations have important impacts on conservation, biodiversity and management of many wild animals and plants. Many fragmented forests have suffered further degradation, hindering forest

regeneration, because seed dispersal and colonization are very poor for many animal-dispersed tree species due to local extinction or rarity of animal seed dispersers (Wunderle, 1997; Corlett, 2002; Duncan and Chapman, 2002). There are at least three aspects considering natural forest restoration in a given fragmented forest: (1) whether potential animal seed dispersers are rare (even extinct) for a given tree species (e.g. Wunderle, 1997; Corlett, 2002; Duncan and Chapman, 2002); (2) whether seed sources are limited

* Corresponding author. Tel.: +86-10-62556418;
fax: +86-10-62565689.
E-mail address: zhangzb@panda.ioz.ac.cn (Z. Zhang).

for a given tree species where potential animal seed dispersers may be abundant (e.g. Wunderle, 1997; Corlett, 2002, Duncan and Chapman, 2002); (3) whether forest fragmentation may lead to reduce or increase seed predator populations (e.g. Nupp and Swihart, 1998, 2000; Goheen and Swihart, 2003). Animal seed dispersal, a dominant mechanism of dispersal in many temperate and tropical forests, has the potential to accelerate forest regeneration and restoration (Howe and Smallwood, 1982; Wunderle, 1997). However, few studies have evaluated the role of seed dispersal by animals (especially scatterhoarding rodents) in forest restorations (e.g. Goheen and Swihart, 2003; Steele et al., in press) or in grassland recovery (e.g. Longland et al., 2001).

Many seed-caching rodents are important seed dispersers for natural regeneration of many nut-bearing tree species by scatterhoarding seeds and nuts in surface soil (e.g. Price and Jenkins, 1986, Miyaki and Kikuzawa, 1988; Vander Wall, 1990, 1993, 1994, 2001; Forget and Milleron, 1991; Forget, 1992, 1993; Brewer and Rejmánek, 1999; Jansen and Forget, 2001; Theimer, 2001; Zhang and Wang, 2001; Hoshizaki and Humle, 2002; Li and Zhang, 2003). It is possible that seed-caching rodents (and other seed-dispersing animals as well) can help restore tree diversity in fragmented forests (see Wunderle, 1997). Therefore, it is needed to evaluate the potential contributions of these animals to forest restoration. Whether a given tree species benefits from the dispersal by seed-caching rodents or other animal seed dispersers depends on: (1) the number of the dispersed seeds from seed sources, e.g. parent plant; (2) the proportion of seeds consumed and cached after dispersal; (3) dispersal patterns (i.e. scattered or clumped); (4) post-dispersal seed shadows (i.e. spatial patterns of the dispersed seeds); (5) seed deposition patterns (e.g. substrates and microsites) (see also Schupp, 1993). In this study, we aimed to quantify the former four aspects of seed dispersal by scatterhoarding rodents, and the fifth one was as Wang et al. (in press). We are also interested in the differences of seed fates (proportion of consumption, removal, caching, missing and survival of seeds) between different dispersal stages, i.e. from seed sources to seedling establishment sites. These are also seldom examined by previous studies (see Vander Wall, 1994, 2002, Jansen, 2003).

In China (and other parts of the world as well), many temperate and tropical forests have been fragmented by agricultural and industrial development, with only small parts remaining as natural forests (Chen et al., 1997). Potential efforts and costs are involved in accelerating forest restoration and regeneration for environmental protection, biodiversity conservation and sustainable development (see Duncan and Chapman, 2002). In the belt of subtropical evergreen broadleaved forest (altitude, 700–1500 m) in the Dujiangyan Region of Sichuan Province, China, many forests are isolated and fragmented by agricultural development and the populations of many common tree species are becoming very rare or extinct due to deforestation (Chen, 2000). For example, oil tea *Camellia oleifera* (Theaceae), an economically important evergreen shrubs or short trees, have been widely distributed for a long time in the Dujiangyan Region, but the populations have been declined sharply due to severe deforestation. Only a small part of oil tea population exists in the primary stands (over 80–90 years) in this region, populations in secondary stands (<50 years) and shrublands (ca. 10 years) being nearly extinct. Seed-caching rodents (e.g. Edward's long-tailed rats *Leopoldamys edwardsi*) are as much as abundant in secondary stands as in primary stands, but seeding regeneration based on 1-year seedlings survey in secondary stands is very poor (nearly zero) comparing with primary stands (Xiao et al., 2002; Xiao, 2003, Z-S Xiao, personal observation). We speculate that poor seeding regeneration of oil tea may be caused by poor seed sources (e.g. few/no fruiting oil tea trees) and subsequent high rodent predation in fragmented secondary forests (see Wunderle, 1997; Corlett, 2002; Duncan and Chapman, 2002). We tested this hypothesis by mimicking natural seed rain.

In this study, we use oil tea as target tree species to examine the role of seed-caching rodents in seeding regeneration in a fragmented secondary forest. Oil tea grows widely in the forests of South and Southwest China as native homeland, and it is also cultivated in economic stands for its commercial tea oil (from seeds), medicinal and industrial uses (Lin and Li, 1989; Zhang, 1998). The flowering period of oil tea coincides with its previous fruit-ripening period, i.e. from September to the November. After ripening, oil tea fruits can naturally dehisce and the seeds inside fall

on the ground under or near parent trees. Sometimes oil tea fruits as a whole fall on the ground. Oil tea fruits are capsules, and every fruit often has 1–8 seeds (mean \pm S.D. g, 0.9 ± 0.3 g, range 0.3–2.0 g, $n = 40$). Oil tea seeds are strictly rodent-dispersed (but not bird-dispersed), and natural regeneration depends largely on seed-caching rodents in the study site (e.g. primary stands) (Xiao, 2003, Z-S Xiao, personal observation). In order to assess the potential benefits of oil tea from the dispersal of seed-caching rodents, we tracked the individual oil tea seeds with coded tin tags by establishing artificial seed sources (mimicking natural seed rain) in a secondary stand, where no oil tea shrubs grow.

2. Study area

We carried out this study in an experimental forest (altitude 700–1000 m, $31^{\circ}4'N$, $103^{\circ}43'E$) from November 2000 to April 2001, in the Dujiangyan City of Sichuan Province, China. Climatically, it lies in the middle subtropical zone, with a mean annual temperature of $15.2^{\circ}C$, and an annual precipitation of 1200–1800 mm (Chen, 2000). The weather is often cloudy and foggy, with only 800–1000 mean annual sunny hours and a mean annual relative humidity of more than 80%.

Because of variation in stand age and vegetation structure, the experimental forest can be sorted into three kinds of stands: primary stands (over 80–90 years), secondary stands (<50 years) and shrublands (ca. 10 years). We conducted this study in a secondary stand. In the secondary stands, *Quercus variabilis*, *Q. serrata*, and *Castanopsis fargesii* are dominant canopy trees. The understory layer is mainly composed of *Symplocos stellaris*, *S. laurina*, *Ilex purpurea*, and *Myrsine africana*. Oil tea (*C. oleifera*) shrubs are very rare or non-existing in the secondary stands, but oil tea populations are rich in the primary stands. The ground flora is dominated by *Dicranopteris pedata*. In the study site, at least 10 small nocturnal rodent species are responsible for seed consumption and scatter-boarding of oil tea and other nut-bearing tree species (e.g. *Lithocarpus harlandii*, *Quercus variabilis*, *Q. serrata*, *Cyclobalanopsis glauca*, and *Castanopsis fargesii*) (Xiao et al., 2003a,b, 2001 Xiao and Zhang, in press): Chestnut rats (*Niviventer fulvescens*),

Edward's long-tailed rats (*Leopoldamys edwardsi*), Bower's rats (*Berylmys bowersi*), White-bellied rats (*N. confucianus*), Himalayan rats (*Rattus nitidu*), Norway rats (*R. norvegicus*), Sichuan field mice (*Apodemus latronum*), Chevriér's field mice (*A. chevriéri*), South China field mice (*A. draco*) and Harvest mice (*Micromys minutus*), among which Chestnut rats, Edward's long-tailed rats, Bower's rats and White-bellied rats, were dominant species (Xiao et al., 2002). In addition, these rodent species prefer more to cache high-value seeds (i.e. oil tea seeds) and larger seeds of *Lithocarpus harlandii* and *Quercus variabilis* (Xiao et al., 2003a; Xiao, 2003). Edward's long-tailed rats, the largest rodents (weight, 200–500 g), have been observed to scatter-hoard oil tea seeds in the soil (Xiao et al., 2003a). During the survey period, we never observed that birds feed on oil tea seeds either on the fruiting trees or on the ground (Z-S Xiao, personal observation).

3. Methods

We selected 800 fresh, sound oil tea seeds collected from parent trees, and labeled them with small modification of the methods by Zhang and Wang (2001). A tiny hole 0.5 mm in diameter was drilled near the germinal disc of each seed. Though the cotyledon was partly damaged, the embryo remained intact and was capable of germinating. A small, light tin-tag ($4\text{ cm} \times 1\text{ cm}$, $<0.1\text{ g}$) was tied through the hole in each seed using an 8 cm thin steel. Each tag was numbered using a fine point metal-pen to make each seed identifiable. When rodents buried the seeds in the soil, the tin-tags were often left on the surface, making them easy to relocate. Tagging had a negligible effect on seed removal and caching by rodents (Zhang and Wang, 2001, Xiao and Zhang, unpublished data).

In a secondary stand (aspect, $30\text{--}60^{\circ}$; direction, southeast; area, 2.5 ha), 20 plots (1 m^2 , area) were established as artificial seed sources, and spaced 10 m apart along a transect line. On 23 November 2000, we released 40 tagged seeds and distributed them evenly at each seed source, which mimics natural seed rain under a fully fruiting tree (Z-S Xiao, unpublished data). After seed release, we checked the tagged seeds at each artificial seed source to investigate seed harvest (i.e. eaten in situ and removal) by small rodents. At the

same time, we randomly searched the area around each artificial seed source (radius, at least 20 m) with equal efforts (3–4 h for two people each visit), for the tagged seeds and their fragments dispersed from each seed source by rodents. We frequently checked all the seed sources and their surrounding area, and all cache sites relocated in previous visits as well. The checking frequency was 1, 2, 3, 4, 6, 8, 10, 14, 18, 156 days after seed release. Post-dispersal seed fates can be sorted into three categories: cached (including buried intact in the soil and deposited intact on the surface), eaten leaving only tin-tags and seed fragments, and missing with their true fates unknown. When we found a cache, we carefully retrieved the seeds, recorded their caches and seed code numbers, and measured the distance of the tagged seeds or their fragments to their original seed source. We then reburied the seeds in the cache site and attempted to keep the disturbance of the caches to a minimum. We used bamboo sticks (10 cm from the cache sites) coded with the number of the relocated seeds to mark cache locations. The marked sticks possibly gave rodents some cues for pilfering, but we found that the marked sticks have few effects on cache survival by establishing artificial caches (Xiao and Zhang, unpublished data). During the next visit, we also checked all the caches relocated in previous visits until the caches were removed or eaten by rodents. If a marked cache was removed, the area around the cache (radius, ≤ 10 m) was randomly searched. When a seed in a primary cache (i.e. after removal from the original seed source) or higher order cache (e.g. secondary cache after primary caches, see Vander Wall, 2002) 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. On April 28, 2002, we surveyed all previously found cache sites to determine whether some of the cached seeds survived to germinate. During the survey, we also mapped the locations for all cache sites.

4. Results

Small rodents harvested all the tagged seeds within 6 days (mean \pm S.D., 2.0 ± 1.2 d, $n = 200$) after being released at artificial seed sources: 67 seeds eaten in situ (8.4%, 3.4 ± 5.1 seeds, range, 0–20 seeds,

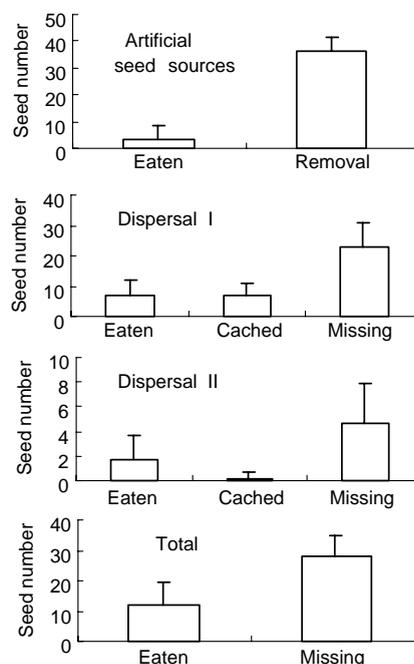


Fig. 1. Fates of the tagged seeds of oil tea during Dispersal I (i.e. from seed stations to primary caches, $n = 800$ seeds) and Dispersal II (i.e. from primary caches to secondary caches, $n = 132$).

$n = 20$) and 733 seeds removed (91.2%, 36.7 ± 5.1 seeds, range, 20–40 seeds, $n = 20$) (Figs. 1 and 2).

During the survey, we relocated 37.4% (274/733) of the removed seeds at least once through random search. During Dispersal I (i.e. from seed stations to primary caches), the fates of the tagged seeds varied across artificial seed sources: eaten (7.1 ± 4.7 seeds, range, 1–21 seeds, $n = 20$), cached (6.6 ± 4.1 seeds, range, 0–17, $n = 20$) and missing (23.0 ± 7.9 seeds, range, 10–38 seeds, $n = 20$). By pooling all data from 20 artificial seed sources, 16.5% of the seeds were cached in primary caches, while the rest were eaten or missing (Fig. 2). We also found that four seeds (0.5%) in primary caches were excavated and recached into secondary cache sites (which were finally eaten or missing), while other seeds in primary caches were eaten or missing during Dispersal II (i.e. from primary caches to secondary caches) (Fig. 2).

As small rodents repeatedly handled the tagged seeds, the proportions of seed consumption (i.e. eaten) and removal were constant in both Dispersal I and Dispersal II (G -test, $G = 0.008$, $df = 1$, $P = 0.985$ for eaten seeds; $G = 0.298$, $df = 1$, $P = 0.385$ for

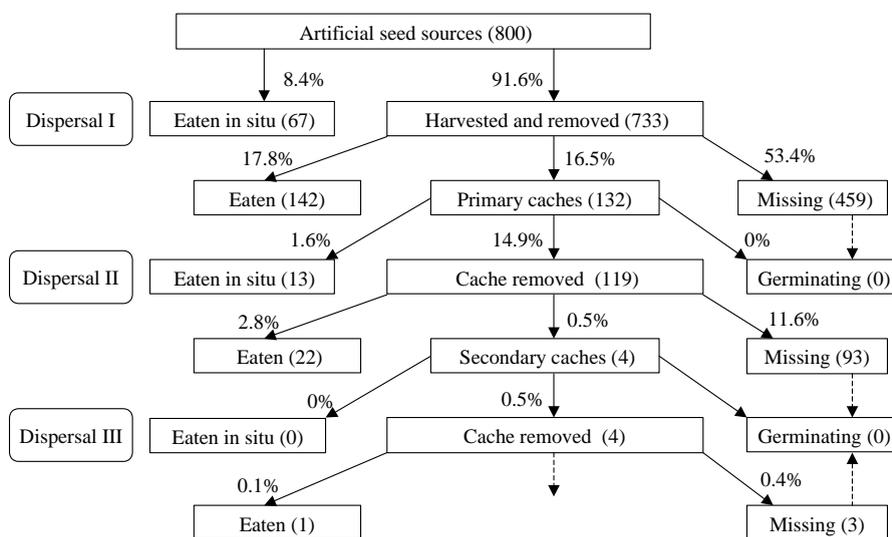


Fig. 2. Fate pathways of oil tea seeds placed in 20 artificial seed sources harvested by small rodents (after Price and Jenkins, 1986). Broken arrows indicate that the possible pathways were not examined in this study. Dispersal I (i.e. from seed stations to primary caches, $n = 800$ seeds), Dispersal II (i.e. from primary caches to secondary caches, $n = 132$) and Dispersal III (i.e. after secondary caches, $n = 4$).

removed seeds), but the proportion of caching significantly decreased (G -test, $G = 21.985$, $df = 1$, $P < 0.001$) and the proportion of missing significantly increased (G -test, $G = 8.262$, $df = 1$, $P = 0.004$) (Figs. 1 and 2). At the end of the survey (28 April 2001), the total eaten proportion of the tagged seeds was 30.6% (12.3 ± 7.3 seeds, range, 2–28 seeds,

$n = 20$), and the missing proportion was higher, amounting to 69.4% (27.8 ± 7.3 seeds, range, 12–38 seeds, $n = 20$) (Fig. 2).

We found 112 caches: 108 primary caches and four secondary caches (Fig. 3). 81.3% (91/112) of the caches (including primary and secondary caches) contained only one seed. We also found that the seeds

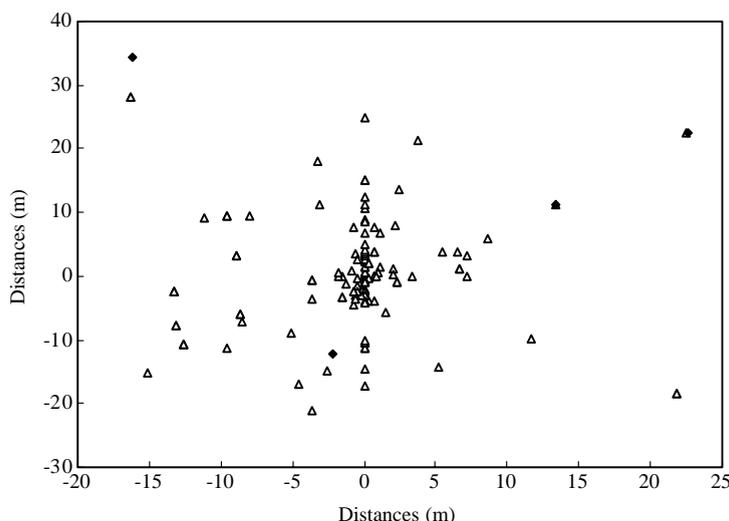


Fig. 3. Spatial patterns of 112 caches around artificial seed sources (pooled data from 20 artificial seed sources). Open triangles are primary caches ($n = 108$), closed diamond squares are secondary caches ($n = 4$).

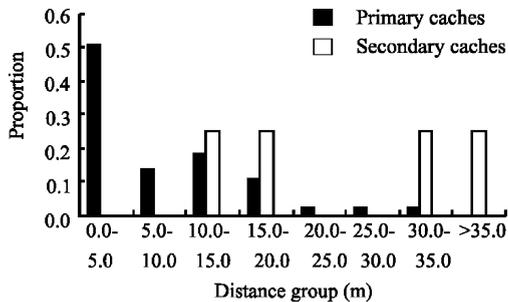


Fig. 4. Frequency distributions of dispersal distances of the tagged seeds in different order caches (i.e. primary and secondary) from artificial seed sources.

in some bigger caches (≥ 2 seeds) came from different seed stations (three cases). Mean cache size of primary and secondary caches was 1.2 ± 0.5 (range, 1–4, $n = 108$) and 1 ± 0 (only one seed in each cache, $n = 4$), respectively.

Almost all caches were ephemeral, including primary and secondary caches. All caches but one primary cache, were eaten or missing within 18 days after seed release, and no seeds survived to germinate in either primary caches or secondary caches in the spring (April) of 2001 (Fig. 2). Mean lifetime of the cached seeds was 4.9 ± 13.3 days ($n = 132$) at primary caches and 2.3 ± 1.3 days ($n = 4$) at secondary caches. 91.9% of the cached seeds were found within 20 m around artificial seed sources (Figs. 3 and 4). The maximum dispersal distance noted of the cached seeds was 38 m, but that of the eaten seeds was 65 m. Though small sampling of the seeds in secondary caches, seed dispersal distances in primary caches (7.9 ± 7.4 m, range, 0–32.5 m, $n = 132$) were significantly shorter than those in secondary caches (25.0 ± 12.0 m, range, 12.5–38.0 m, $n = 4$) ($P < 0.05$, Mann–Whitney U -test). The intercache distances were 12.8 ± 9.2 m (range, 2–23 m, $n = 4$) between primary and secondary caches.

5. Discussion

We found the total survival of the released seeds was zero (Fig. 2). This result confirms the hypothesis that poor seeding regeneration may be caused by high rodent predation in the fragmented secondary forest, where there were poor seed rain of oil tea due to few

no fruiting trees. This observation also supports the statement that the efficacy of animal seed dispersal to restoration sites can be limited by poor seed sources and high seed predation in fragmented forests (e.g. Wunderle, 1997; Corlett, 2002, Duncan and Chapman, 2002). In *Camellia*-poor stands, seed consumption is high (22.3%) during dispersal stages (Fig. 2), which potentially reduce absolute or relative survival of the removed seeds (especially the cached seeds). Moreover, most of the missing seeds (ca. 70%, Fig. 2) are likely to be eaten somewhere (e.g. underground burrows). There may be three kinds of fates for these missing seeds (see Vander Wall, 2002). First, most of these seeds may have been transported to underground burrows, rock caves and dense shrubs (larder-hoarded), where we cannot reach them. Second, small rodents may also have transported some seeds beyond the survey area because some seeds were cached 38 m from seed sources or eaten 65 m from seed sources. Third, some seeds may survive to germinate, but they have not been examined during the survey.

The differences of seed fates among different dispersal stages have hardly been assessed. We found that the proportions of consumption (i.e. eaten) and removal were constant in both Dispersal I and Dispersal II, but the proportion of caching significantly decreased and the proportion of missing significantly increased, as rodents repeated handled the cached seeds (Figs. 1 and 2). The buried seeds were as easily discovered as the released seeds on soil surface by rodents, indicating that the buried seeds were probably harvested again by the same host rodents. Seed burying can effectively reduce seed harvest by the non-host rodents. Nearly all caches are very ephemeral (mean lifetime, less than 5 days) because small rodents excavate the scatter-hoarded seeds frequently. We did not observe the increase of seed survival in the later dispersal stage. The less proportion of caching in the later dispersal stage was probably due to transportation of seeds to their burrows by rodents, which contributed higher missing proportion of seeds in the later stage.

However, our observation does not mean that rodents are not important in promoting natural regeneration of oil tea through seed dispersal by seed-caching rodents. High seed removal (91.2%) and quick harvest mean that more seeds are more likely to be cached somewhere from seed sources, rather

than instant seed consumption (see also Jansen and Den Ouden, in press). We found that all 40 tagged seeds were removed at six of 20 artificial seed sources just the night after seed release. The seed removal rate in this study is very like natural removal (over 90%) under parent plant in primary stands (Xiao, 2003). Many removed seeds were found to be cached in the surface soil (48.2% for the relocated seeds), indicating that seed removal is not equal to seed predation (Forget, 1992; Jansen and Den Ouden, in press). Seed scatter-hoarding (including repeated caching) by small rodents can reduce seed density around seed sources, and potentially extend seed shadows (e.g. distances to seed sources and cache spacing) (Jansen and Forget, 2001; Vander Wall, 2002, 2003). Oil tea seedlings can benefit from one-seed caches (81.3%), indicating few or no competitions from siblings. Therefore, seed-caching rodents could have the potential to help restore natural populations of oil tea in the *Camellia*-rich stands (e.g. in primary stand).

There are two main methods to increase seed sources: tree plantations and direct seeding (see Wunderle, 1997; Duncan and Chapman, 2002). In the early period of oil tea restoration, both tree planting and direct seeding may be very effective to increase oil tea seeds, since the growth period of oil tea is relatively short (only 5–6 years) from seeds to fruiting shrubs (Lin and Li, 1989; Zhang, 1998). In this study, increasing seed sources of oil tea in the secondary forest should be taken as the first priority. Other considerations are also needed to guarantee the effectiveness of restoration efforts, e.g. the distributions and numbers of seed sources, stand area, understory structures and the period of seed release. It is very essential to explore some economical methods (e.g. natural seed dispersal) to accelerate forest restorations, because the restoration costs (e.g. tree planting and direct seeding) are very expensive. These remain to study in the future.

Acknowledgements

Mark V. Price, Stephen B. Vander Wall and Pierre-Michel Forget made critical comments and suggestions on the early version of this manuscript. We also thank two anonymous reviewers for their valuable comments and Jason and Ruihua Lei for English

writing to our manuscript. This study was funded by state key project of CNSF (G2000046802), and the innovation programs of CAS (KSCX2-SW-105 and KSCX2-SW-103). We thank the Subalpine Mountain Plant Garden of West-China, CAS, and the Forest Bureau of Dujiangyan City, Sichuan Province, for much support for our field investigation.

References

- Brewer, S.W., Rejmánek, M., 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *J. Veg. Sci.* 10, 165–174.
- Chen, C.-D., 2000. Biodiversity Research and Conservation of Dujiangyan, China. Sichuan Science and Technology Press, Chendu, in Chinese.
- Chen, L.-Z., Chen, Q.-L., Liu, W.-H., 1997. Forest diversity and its geographical distribution in China. Science Press, Beijing.
- Corlett, R.T., 2002. Frugivory and seed dispersal in degraded tropical East Asian landscapes. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, pp. 451–465.
- Duncan, R.S., Chapman, C.A., 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, pp. 437–450.
- Forget, P.-M., 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24, 408–414.
- Forget, P.-M., 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papi-lionaceae) seeds by rodents in Panama. *Oecologia* 94, 255–261.
- Forget, P.-M., Milleron, T., 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87, 596–599.
- Goheen, J.R., Swihart, R.K., 2003. Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: implications for forest regeneration. *Can. J. Zool.* 81, 1636–1639.
- Hoshizaki, K., Humle, P.E., 2002. Mast seeding and predator-mediated indirect interactions in a forest community: Evidence from post-dispersal fate of rodent-generated caches. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, pp. 227–239.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201–228.
- 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., Den Ouden, J., Actors of post-dispersal seed removal and their behaviour: video monitoring seed predation and

- secondary dispersal. In: Forget, P.-M., Lambert, J., Hulme, P.E., Vander Wall, S.B. (Eds.), Seed fates: seed predation, seed dispersal and seedling establishment. CABI Publishing, Wallingford, in press.
- Li, H.-J., Zhang, Z.-B., 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). *Forest Ecol. Manage.* 176, 387–396.
- Lin, S., Li, G., 1989. Production situations and developmental strategies of oil tea in China. *World Forest Res.* 4, 70–75 (in Chinese).
- Longland, W.S., Jenkins, S.H., VanderWall, S.B., Veech, J.A., Pyare, S., 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* 82, 3131–3148.
- Miyaki, M., Kikuzawa, K., 1988. Dispersal of *Quercus mongolica* acorns in a broad-leaved deciduous forest. Part 2. Scatterhoarding by mice. *Forest Ecol. Manage.* 25, 9–16.
- Nupp, T.E., Swihart, R.K., 1998. Influence of forest fragmentation on population attributes of white-footed mice and eastern chipmunks. *J. Mammal.* 79, 1234–1243.
- Nupp, T.E., Swihart, R.K., 2000. Landscape-level correlates of small mammal assemblages in forest fragments of farmland. *J. Mammal.* 81, 512–526.
- Price, M.V., Jenkins, S.H., 1986. Rodents as seeds consumers and dispersers. In: Murray, D.R. (Ed.), *Seed Dispersal*. Academic Press, Sydney, pp. 191–235.
- Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetation* 107–108, 15–29.
- Steele, M., Wauters, L.A., Larsen, K.W., Selection, predation and dispersal of seeds by tree squirrels in temperate and boreal forests: are tree squirrels keystone granivores? In: Forget, P.-M., Lambert, J., Hulme, P.E., Vander Wall, S.B., (Eds.), *Seed fates: seed predation, seed dispersal and seedling establishment*. CABI Publishing, Wallingford, in press.
- Theimer, T.C., 2001. Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *J. Trop. Ecol.* 17, 177–189.
- Vander Wall, S.B., 1990. *Food Hoarding in Animals*. University of Chicago Press, Chicago.
- Vander Wall, S.B., 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia* 96, 246–252.
- Vander Wall, S.B., 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 75, 1911–1926.
- Vander Wall, S.B., 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67, 74–117.
- Vander Wall, S.B., 2002. Secondary dispersal of Jeffrey pine seeds by rodent scatter hoarders: the roles of pilfering, recaching, and a variable environment. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, pp. 193–208.
- Vander Wall, S.B., 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* 100, 25–34.
- Wang, Y.-S., Xiao, Z.-S., Zhang, Z.-B., Seed deposition of oil tea *camellia oleifera* influenced by seed-caching rodents. *Acta Botanica Sinica*, in press.
- Wunderle Jr., J.M., 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecol. Manage.* 99, 223–235.
- Xiao, Z.-S., 2003. Effects of small mammals on tree seed fates and forest regeneration in Dujiangyan Region, China. Ph.D. Thesis, Institute of Zoology, Chinese Academy of Sciences, Beijing (in Chinese with English summary).
- Xiao, Z.-S., Wang, Y.-S., Zhang, Z.-B., Ma, Y., 2002. Preliminary studies on the relationships between communities of small mammals and types of habitats in Dujiangyan Region. *Chinese Biodiv.* 10, 163–169 (in Chinese with English summary).
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2003a. Observations on tree seed selection and caching by Edward's long-tailed rat (*Leopoldamys edwardsi*). *Acta Theriologica Sinica* 23, 208–213 (in Chinese with English summary).
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2003b. The ability to discriminate weevil-infested nuts by rodents: potential effects on regeneration of nut-bearing plants. *Acta Theriologica Sinica* 23, 312–320.
- Xiao, Z.-S., Zhang, Z.-B., Small mammals consuming tree seeds in Dujiangyan forest. *Acta Theriologica Sinica* (in Chinese with English summary), in press.
- Zhang, R., 1998. *Chinese oil tea*. Chinese Forestry Press (in Chinese).
- Zhang, Z.-B., Wang, F.-S., 2001. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Ecol. Sinica* 21, 839–845.