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SCIENCE DIRECT
Acta Oecologica 26 (2004) 247–254
ACTA OECOLOGICA
INTERNATIONAL JOURNAL OF ECOLOGY
www.elsevier.com/locate/actoec

Original article

Effects of habitat and season on removal and hoarding of seeds of wild apricot *(Prunus armeniaca)* by small rodents

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Received 4 December 2003; accepted 7 August 2004

Available online 11 November 2004

Abstract

The wild apricot *(Prunus armeniaca)* is widely distributed in the Donglingshan Mountains of Mentougou District of Beijing, China, where its seeds may be an important food resource for rodents. Predation, removal and hoarding of seeds by rodents will inevitably affect the spatio-temporal pattern of seed fate of wild apricot in this area. By marking and releasing tagged seeds of wild apricot, we investigated seeds survival, scatter-hoarding, cache size and seedling establishment, and the preference of micro-habitats used by rodents to store seeds. The results showed that: (1) rodents in this area hoarded food intensively in autumn, as well as in spring and summer. (2) There were significant effects of habitat and season on removal rate of tagged seeds at releasing plots. In both two types of habitats, Low and High shrub, tagged seeds were removed most rapidly by rodents in autumn, at intermediate rates in spring and least rapidly in summer. (3) During three seasons, mean dispersal distance of scatter-hoarded seeds in Low shrub habitat was greater than that in High shrub. Most removed seeds were buried within 21.0 m of the releasing plots. (4) In both two types of habitats, Low and High shrub, rodents tended to carry seeds to US (Under shrub) and SE (Shrub edge) microhabitats for scatter-hoarding or predation. (5) Among the caches made by rodents, most caches contained only one seed, but up to three seeds were observed; caches of 2–3 seeds were common in autumn. (6) By comparing dental marks, we determined that large field mice *(Apodemus peninsulae)* and David's rock squirrels *(Sciurotamias davidianus)* contributed to removal and predation of released tagged seeds. However, only the large field mice exerted a pivotal and positive role on the burial of dispersed seeds. (7) Establishment of three seedlings originated from seeds buried by rodents was documented in High shrub habitat.

Keywords: Wild apricot *(Prunus armeniaca)*; Rodents; Removal; Hoarding; Habitats; Season; Cache size

1. Introduction

Scatter-hoarding animals, e.g. rodents, have important impacts on seedling establishment and plant regeneration by burying seeds and nuts in soil away from the parent plant (Morris, 1962; Abbott and Quink, 1970; Smith and Reichman, 1984; Vander Wall, 1990, 1993; Forget and Milleron, 1991; Longland and Clements, 1995; Vander Wall et al., 2001). Indeed, while buried seeds are not all retrieved by hoarders or other individuals in the future, some may germinate and establish seedlings under favorable conditions (Vander Wall, 1990, 1993). Thus, scatter-hoarding may play a positive role in seedling establishment and plant regeneration (Jensen and Nielson, 1986; Vander Wall and Joyner, 1998; Price et al., 2000; Forget and Vander Wall, 2001).

Seed dispersal is the first step in a multistage process leading to plant regeneration. Many pre- and post-dispersal factors, such as seed characteristics and environmental factors, have been examined to affect seed hoarding behaviour of rodents (Vander Wall, 1990), and subsequent seedling recruitment (Duncan and Chapman, 1999). Several studies suggested that heterogeneity of habitats might affect the distribution and foraging activities of rodents, and thus exert different effects on the spatial pattern of dispersal and survival of seeds (Kollmann and Schill, 1996; Rusell and Schupp, 1998). In habitats with poor shelter, animals may carry seeds longer distances to find "secure" sites to hoard

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doi:10.1016/j.actao.2004.08.002

their food resource (MacDonald, 1976; Vander Wall, 1990). Although season and habitat (time and space) are two important factors influencing food hoarding in animals, we are not aware of any study in which seed removal and hoarding were compared among seasons and habitats in temperate regions. Though many studies have showed that seed-caching rodents in temperate regions hoard seeds and nuts intensively in autumn (Vander Wall, 1990), few studies have considered whether these rodents hoard seeds and nuts in spring and summer.

Despite the significance of scatter-hoarding by rodents, we still have very limited knowledge about seed removal and hoarding. One of the reasons is the difficulty of tracking the fate of removed and buried seeds (Sork, 1984). Zhang and Wang (2001) developed a new method of labeling seeds with small pieces of tin tags. The tin-tagged seeds are individually coded and easily identified. This method makes it possible to determine the location and fate of seeds that were dispersed and buried, or eaten by rodents.

Wild apricot *(Prunus armeniaca)*, commonly seen in deforested hills, is distributed widely in the Donglingshan Mountains of Mentougou District of Beijing (provincial city), China. This plant is the dominant species in wild apricot shrubland, or the subdominant or concomitant in other types of shrublands on dry-sunny slopes (Ma et al., 1997). The wild apricot is a pioneer species in succession on deforested sites (Zhang and Wang, 2001). The seed of wild apricot is ovoid in shape with biconvex sides. Owing to their high nutritional value, seeds of wild apricot are preferred food resources for small rodents (Chen et al., 2002). Because of a hard endocarp, seeds of wild apricot can be stored for long periods. During the fruiting period, rodents may remove and store seeds of wild apricot for the future when food supply is poor, i.e. winter. Studies conducted in this area showed that rodents, such as large field mice *(Apodemus peninsulae)*, Chinese white-bellied rats *(Niviventor confucianus)*, David's rock squirrels *(Sciurotamias davidianus)* and greater long-tailed hamsters *(Cricetulus triton)* might prey upon and remove artificially released seeds of wild apricot (Zhang and Wang, 2001; Li, 2002). However, we know little about the exact role of different rodent species playing in its seed ecology.

The two objectives of this study were: (1) to test whether rodents also hoard in spring and summer, and whether they hoard more seeds in autumn; and (2) to test whether rodents remove and hoard seeds differently among micro-habitats. This study also aims to determine: (1) the main species of rodents acting on seeds of wild apricot; (2) the distribution pattern of seeds buried by rodents in different seasons and habitats; (3) the distances of buried seeds from the point where they were released; and (4) cache size of scatter-hoarded seeds of wild apricot. Answering these questions will enhance our understanding of the interactions between rodents and seeds of wild apricot, and support recommendation regarding restoration and management of human-disturbed deforested ecosystems.

2. Methods

2.1. Study site

This study was conducted in a mountainous area, at an altitude about 1140 m, near Liyuanling Village in Mentougou District of Beijing (provincial city), and about 120 km northwest of Beijing City, China (40°00′N, 115°30′E). This area is in the Donglingshan Mountains, with a temperate continental monsoon climate. Vegetation of the study area has been heavily disturbed by local residents and domestic animals for almost a century. In this area the main types of vegetation are shrublands, abandoned farmland and secondary forests. The plant community consists of a sparse stand of Liaodong oak *(Quercus liaotungensis)*, wild walnut *(Juglans mandshurica)*, wild apricot *(Prunus armeniaca)* and larch *(Larix principis-rupprechtii)*. Young Liaodong oak, the elm *(Ulmus laciniata)*, and wild apricot are common species in the shrub community (Li and Zhang, 2003).

2.2. Selection of experimental plots

We chose shrub habitats as our sample area and classified them into two types according to plant height: (1) in Low shrub, dominant species were *Spiraea pubescens* and *Vitex negundo*, with an average plant height of 79.6 cm and average coverage of 44.7%. This habitat is located on southwestern-facing slopes with a gradient of 45°–50°; (2) in High shrub, dominant species were *Ulmus laciniata* and Liaodong oak, with an average plant height of 210.7 cm and average coverage of 76.3%. This habitat is located on southwestern-facing slopes with a gradient of 30°–45°. Each type of habitat was about 2 ha in area. Within the two habitats, we sampled two transects along the slope direction. Along each transect, we sampled 15 experimental plots 10 m apart. We also recorded micro-habitat ecological factors such as gradient, plant height and coverage level, in 1 m^2 in each plot.

2.3. Seed marking and releasing

During the fruiting period of the previous year, intact and mature endocarps of wild apricot were collected for use in experiments. Seeds weighed 1.00 ± 0.24 g, and measured 2.08 ± 0.14 cm × 1.73 ± 0.11 cm × 0.93 ± 0.01 cm. To mark endocarp without destroying kernels, tiny holes were drilled at the base of each endocarp. A small, light tin-tag (≈3.5 × 1 cm, < 0.1 g) was tied to each endocarp through the hole with a fine steel wire 3 cm long, and the tags were coded using a sharpened metal-pen (Zhang and Wang, 2001; Li and Zhang, 2003). When rodents buried seeds in soil, the tin-tags were often visible on the surface, making them easy for us to relocate. Prior preliminary studies showed that the metal-tagged seeds were removed as readily as unmarked seeds. Thus, the experimental treatment yields realistic results on the movement pattern of seeds of wild apricot.

In spring (14 April 2002), summer (7 July 2002) and autumn (10 October 2002), 40 tagged seeds were placed on the ground surface within the nearby 1 m^2 plots selected along the two transects. The total number of tagged seeds for the three seasons was 2 (habitat) × 3 (season) × 15 (plots) × 40 seeds = 3600 seeds. The next day after placement, we checked every plot to determine if the tagged seeds remained or had been removed by rodents. We also searched (within 50 m of origin) for tagged seeds that had been taken away. Once a tagged seed was found, we recorded its code, position, distance from plot, status of seed, and the types and environmental characteristics of micro-habitat within 1 m^2 of its location. We checked the experimental plots for 16 days successively, after the seeds were released.

The removed seeds were defined as follows: (1) hoarded (H): the tagged seed was buried with the tin-tag being visible above the soil surface; (2) eaten after removal (E): a gnawed hole left by rodent on the tagged seed and the kernel removed, only the seed coat being left on the ground surface with the attached tin-tag; (3) missing (M): the tagged seed was not found after removal; and (4) surface (S): the tagged seed was removed from the releasing plot and left intact on the ground surface. The micro-habitats where seeds were found buried or eaten included four categories defined as follows (Li and Zhang, 2003): (1) under shrubs (US): the tagged seed was buried in soil or scattered on the ground surface under shrub cover; (2) shrub edge (SE): the tagged seed was buried in soil or scattered on the ground surface at the edge of shrub cover; (3) grass (G): the tagged seed was buried in or scattered on open grass; and (4) bare ground (BG): the tagged seed was buried in or scattered on bare ground.

2.4. Rodent identification and density

Rodent predation left obvious scrapes and dental marks on endocarps of wild apricot. Dental marks left by different species of rodents were distinguishable, enabling identification of the predator of each seed (Fig. 1).

To minimize the influence of trapping on rodent population density in the study area, we selected two communities similar to our study transects (about 500 m away from transects) to survey rodent densities. Wooden snap traps baited with peanuts were used every season. Twenty-five traps were set in each selected communities at an interval of 5 m. The traps were checked daily for 2 days and the captured rodents were measured and recorded.

2.5. Statistics and analysis

SPSS (Version 10.0) for Windows was employed for statistical analysis. Survival dynamics of tagged seeds at releasing plots were analyzed. Two-way ANOVA was used to test for the difference of dispersal distance of buried seeds and survival time of seeds at releasing plots between Low and High shrub and among three seasons, respectively, and for the interaction. Mann-Whitney U tests were used to determine the difference between Low and High shrubs in each of three seasons; Kruskal–Wallis tests were used to determine the differences among three seasons both in Low and High shrubs; and Chi-square tests were used to test whether the hoards were randomly distributed among the four categories of micro-habitats (US, SE, G, and BG).

3. Results

3.1. Seed predators

The results of indoor feeding showed that four species of rodents, i.e. large field mice *(A. peninsulae)*, Chinese white-bellied rats *(N. confucianus)*, David's rock squirrels *(S. davidianus)* and greater long-tailed hamsters *(C. triton)* predated seeds of wild apricot (Table 1). However, we found that large field mice and David's rock squirrels accounted for the dental marks left on seeds collected in the field (Table 1). Moreover, only large field mice were captured in each shrub habitat. We thus concluded that large field mice and David's rock squirrels were the main species of rodents that prey upon seeds of wild apricot in the study area (Tables 1 and 2).

3.2. Effects of habitat and season

The median survival time of tagged seeds at releasing plots was 15 days, in spring and summer in both habitats, and

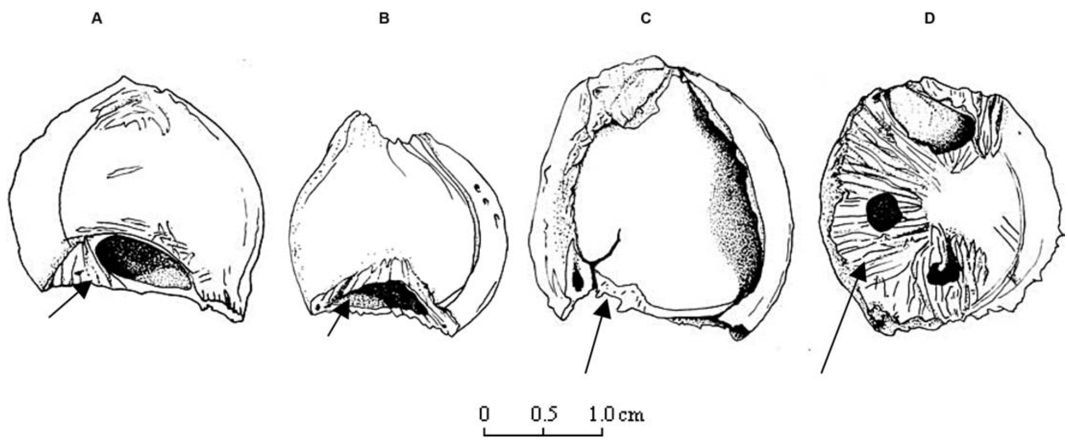

Fig. 1. Characteristics of dental marks left by different species of rodents (a) *A. peninsulae*, (b) *N. confucianus*, (c) *S. davidianus*, (d) *C. triton*.

Table 1
Comparison among characteristics of dental marks made by rodents

Species	Opening size	Number of opening	Position of opening	Edge of opening	Seed coat-remained
Large field mice *Apodemus peninsulae*	Small	1	Lateral	Straight and smooth	Intact
Chinese white-bellied rats *Niviventor confucianus*	Larger	1	Lateral	Inclined and rough	Intact
David's rock squirrels *Sciurotamias davidianus*	Largest	1	Random	Broken	Cracked
Greater long-tailed hamsters *Cricetuls triton*	Small	>2	Random	Rough and scraped	Intact

Table 2
Statistics of seeds consumed by rodents

	Large field mice Apodemus *peinsulae*	Chinese white-bellied rats *Niviventorconfucianus*	David's rock squirrels *Sciurotamias davidianus*	Greater long-tailed hamsters *Cricetulus triton*
Indoor feeding	211	58	8	147
Collected from field	389	0	22	0

5.86 and 8.73 days in Low and High shrub, respectively, in autumn. Overall, seed removal rates differed significantly among seasons ($F = 37.678$, df = 2, $P < 10^{-3}$) and between habitats ($F = 5.100$, df = 1, $P = 0.026$), while the interaction between season and habitat was not significant ($P = 0.252$). Seed removal rate was greater in autumn, intermediate during spring, and lowest during summer in both Low and High shrub (Fig. 2).

3.3. Distance of seed dispersal

During the experiment, some of the released seeds were carried by rodents into certain micro-habitats for scatter-hoarding. The mean dispersal distance of scatter-hoarded seeds in Low shrub was greater than that in High shrub ($F = 9.740$, df = 1, $P = 0.002$) over all seasons, and there was no significant difference in mean dispersal distance among seasons ($P = 0.907$) between habitats. The interaction between season and habitat was not significant ($P = 0.176$). When the effects of habitats and seasons were considered independently, the results showed that the differences in mean dispersal distance of buried seeds were not significant in either Low ($P = 0.069$) and High ($P = 0.951$) shrub. Difference between Low and High shrub were significant both in spring ($P < 10^{-3}$) and autumn ($P < 10^{-3}$), and was insignificant in summer ($P = 0.131$) (Table 3).

Within Low shrub, the percentages of scatter-hoarded seeds dispersed to distances of less than 6.0 m were 57% in spring, 50% in summer and 53% in autumn. The percentages of hoarded seeds with dispersal distances less than 21.0 m were 90.9% in spring, and 100% in both summer and autumn (Fig. 3). Within High shrubs, the percentages of scatter-hoarded seeds with dispersal distance less than 6.0 m were 77% in spring, 57% in summer and 71% in autumn (Fig. 3). In this habitat, almost all of the scatter-hoarded seeds (100% in both spring and summer, and 99.2% in autumn) were dispersed to distances less than 21.0 m (Fig. 3).

3.4. Scatter-hoarding of seeds

3.4.1. Effects of micro-habitats

When removed, most of the tagged seeds of wild apricot were buried, i.e. scatter-hoarded, by the rodents (Table 4). Within Low shrub, the percentages of scatter-hoarded seeds

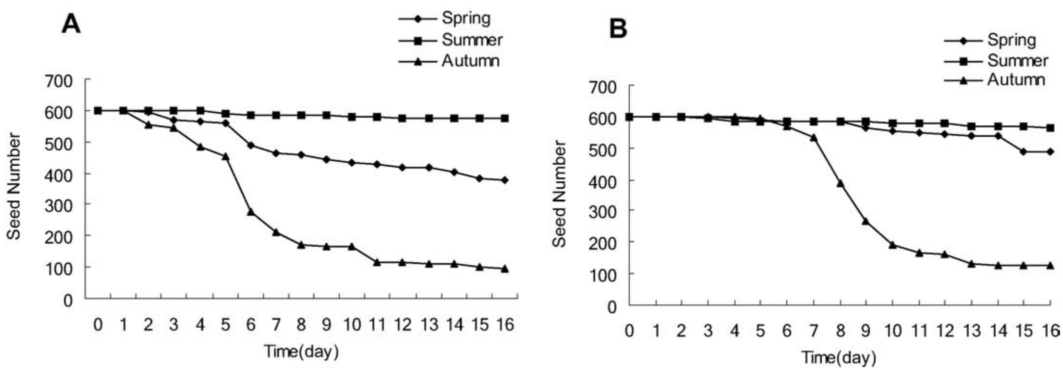

Fig. 2. Survival dynamics of tagged seeds of wild apricot at releasing plots. The seeds were released in spring (14 April 2002), summer (7 July 2002) and autumn (10 October 2002), respectively. The clump size was 40 seeds/plot in every releasing time. (a) Low shrub, plots = 15, No. of seeds = 600; (b) High shrub, plots = 15, No. of seeds = 600).

Table 3
Data on dispersal distance (m) of tagged seeds buried by rodents

Season	Habitat				Mann-Whitney U	
	Low shrub		High shrub		Z	P
	N	Mean ± S.D. (range)	N	Mean ± S.D. (range)		
Spring	44	7.7 ± 6.4 (1.0–26.0)	44	3.9 ± 2.6 (1.0–11.0)	–3.615	0.000
Summer	8	6.2 ± 2.8 (2.7–11.0)	7	4.4 ± 2.2 (2.0–6.9)	–1.511	0.131
Autumn	85	6.7 ± 4.5 (1.0–19.1)	124	4.9 ± 3.3 (0.7–21.9)	–2.579	0.010
Kruskal–Wallis		$\chi^2 = 5.338$		$\chi^2 = 0.101$		
		$P = 0.069$		$P = 0.951$		

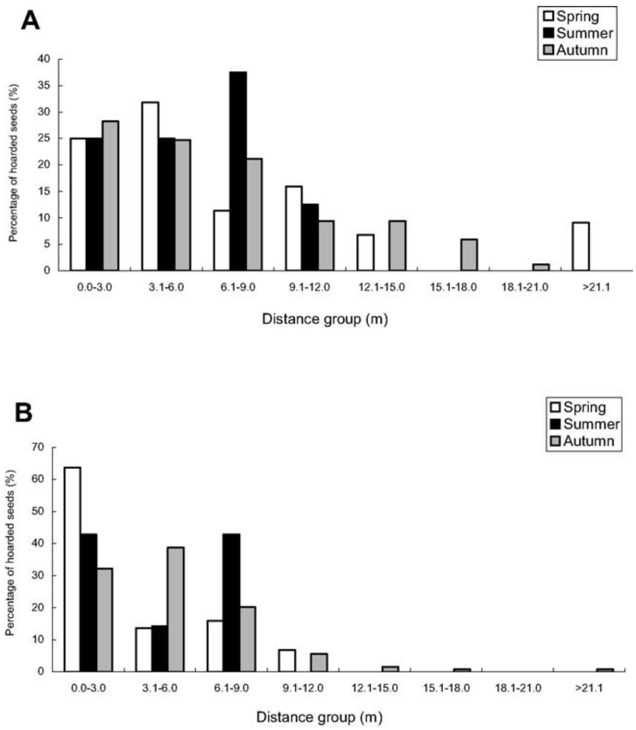

Fig. 3. Proportional distribution of dispersal distances of buried tagged seeds within Low and High shrub in three seasons (a) Low shrub, (b) High shrub).

were 72.1%, 50.0% and 55.9% in spring, summer and autumn, respectively; while the percentages in High shrub were 84.6% in spring, 33.3% in summer, and 72.9% in autumn. The percentages of tagged seeds eaten by rodents after removal were all very low, and the differences were not compared.

Within both Low and High shrub, rodents transported tagged seeds into certain micro-habitats for scatter-hoarding. Most of the seeds cached by rodents were near the releasing plots (Fig. 3). With increasing distance from releasing plots, the number of hoarded seeds decreased within both Low and High shrub and in all three seasons (Fig. 3). When scatter-hoarding seeds, rodents tended to select the micro-habitats of US and SE (Under shrub and Shrub edge), and they did not randomly hoard seeds among the four categories of micro-habitats (Fig. 4). Because very few seeds were scatter-hoarded in summer, in both Low and High shrub habitats, we combined the results for the three seasons for analysis in the two types of habitats. The results showed that the differences in distribution pattern of scatter-hoarded seeds among four categories of micro-habitats were significant in both Low ($P < 10^{-3}$) and High ($P < 10^{-3}$) shrub (Fig. 4), and relatively fewer tagged seeds were carried into grass (G). No tagged seeds were buried in bare ground (BG), either within Low and High shrub, during all three seasons (Fig. 4).

3.4.2. Cache size and seedling establishment

After removing tagged seeds from releasing plots, rodents made a large number of scattered caches. Both within Low and High shrub and in all three seasons, the size of caches was 1–3 seeds. The majority of the caches contained only one seed; caches containing two or three seeds were observed only in autumn, and three-seeds caches were observed only in High shrub habitat. In spring 2003, we checked the caches in study area carefully, and found that almost all buried seeds had been retrieved by rodents. Three seedlings derived from buried tagged seeds had successfully established in the micro-habitats of SE (Shrub edge) in High shrub. The original tagged seeds were all released in spring 2002.

4. Discussion

4.1. Main rodent species interacting with seeds of wild apricot

The main species of rodents that predated seeds of wild apricot at our study sites were large field mice *(A. peninsu-*

Table 4
Number of tagged seeds in each status after dispersal

Habitat	Season	Released	Removed	Surface	Hoarded	Eaten	Missing
Low-shrub	Spring	600	220	15	44	1	159
	Summer	600	27	8	8	0	11
	Autumn	600	503	75	85	0	352
High-shrub	Spring	600	114	8	44	0	62
	Summer	600	35	12	7	1	14
	Autumn	600	475	40	124	3	305

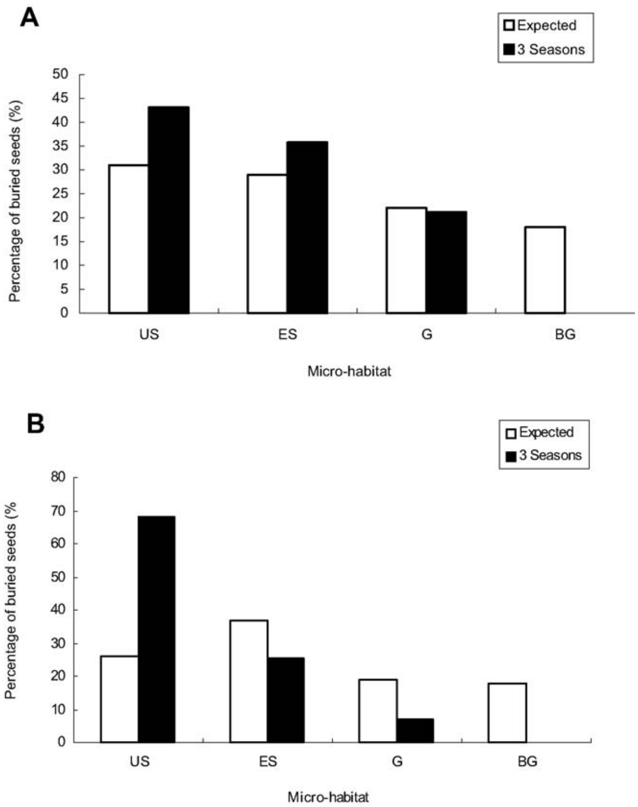

Fig. 4. Distribution of percentages of buried seeds within four categories of micro-habitats in three seasons ((a) Low shrub; (b) High shrub). "Expected" means the proportion of different micro-habitats (Under shrub, US; Shrub edge, SE; Grass, G and Bare ground, BG) in the study transects.

lae) and David's rock squirrels *(S. davidianus)*. The role of David's rock squirrels was neglected in prior studies (Zhang and Wang, 2001; Li, 2002). We believed that large field mice play a pivotal role in the removal and scatter-hoarding of seeds of wild apricot in the study area. Several prior studies in this area showed that Chinese white-bellied rats *(N. confucianus)* and greater long-tailed hamsters *(C. triton)* also predated seeds of wild apricot (Zhang and Wang, 2001; Li, 2002). Comparison of dental marks left on seeds showed that the two last species predate few seeds in the field. We thus concluded that these two species of rodents might play a relatively limited role in removal and scatter-hoarding of tagged seeds at our study area.

4.2. Spatio-temporal variation of seed removal and hoarding

In autumn, the median survival time of tagged seeds at releasing plots within Low shrub was shorter than that in High shrub, while capture rates of large field mice were 4.0% and 0.0% in Low and High shrub, respectively. Heterogeneity of habitats may thus affect densities of rodent populations and consequently exert effects on the spatial pattern of dispersal and survival of seeds (Kollmann and Schill, 1996; Russell and Schupp, 1998).

Although rodents are widely considered not to hoard food during spring in temperate regions (Vander Wall, 1990), we observed that small rodents did remove and scatter-hoard released seeds of wild apricot in spring as well as in summer. Spring food hoarding can be explained by the fact that hoarded food had been heavily consumed during the long winter, and there were few alternative food resources for rodents. They thus removed and hoarded tagged seeds for their exclusive use in the short term. During summer, plants such as wild apricot and wild peach set fruits successively, providing relatively abundant food resources for rodents. Removal and burial rates of tagged seeds thus decreased in summer.

The results of this study showed that seed hoarding by rodents was most prevalent in autumn within both Low and High shrub. The reasons for this phenomenon may be: (1) since a long winter, with a poor food supply, was coming soon, rodents have to store food to cope with possible food scarcity in the future, in other words, the apperceive for a food shortage triggered seed hoarding of rodents in autumn (Vander Wall, 1990); (2) once seed predators encountered seed resources, rapid removal of seeds by the forager is important because this will decrease the probability of those resources being found by other seed predators which also forage on the ground (Vander Wall, 1993; Zhang et al., 1998; Li and Zhang, 2003); and (3) few acorns of Liaodong oak, which serves as food resource for rodents in autumn, were produced in the study area in autumn 2002.

4.3. Dispersal distances of scatter-hoarded tagged seeds

The mean dispersal distance in Low shrub was greater than that in High shrub in all three seasons, and the difference was significant. This indicate that rodents have to carry seeds over longer distances within Low shrub to find secure sites in which to hoard seeds (MacDonald, 1976; Vander Wall, 1990), because of poorer shelter conditions in Low shrub than in High shrub. Relatively open habitat, e.g. Low shrub, may incur higher predation risk for rodents since they can be more easily detected by their predators in such habitats (Lima, 1998). Within both Low and High shrub and during different seasons, most removed seeds were buried within 21.0 m. The number of dispersed seeds decreased with increasing distance from releasing plots (Willson, 1993; Vander Wall, 1997; Li, 2002; Li and Zhang, 2003).

4.4. Micro-habitats where tagged seeds were buried

In this study, rodents tended to select certain micro-habitats such as US (Under shrub) and ES (Shrub edge) to hoard tagged seeds in both Low and High shrub and over all three seasons, while few seeds were carried into micro-habitat of G (Grass), and no seeds were buried in BG (Bare ground). One of the advantages of hoarding seeds near shrubs is that shrubs will provide better shelter for rodents while they are foraging or hoarding, decreasing predation risk (Vander Wall, 1993; Lima, 1998; Li and Zhang, 2003). US and SE microhabitats are also suitable sites for seedling establishment and plant recruitment, because better nutrients, moderate temperatures, and higher soil humidity within these micro-habitats will promote germination of seeds and increase survival of seedlings (Duncan and Chapman, 1999). On the other hand, seeds that were dispersed into certain micro-habitats, such as G and BG with poorer coverage of vegetation, will be more easily found and eaten by seed predators. Furthermore, high temperatures, drought and exposure to ultra-violet radiation within these micro-habitats may also hamper germination and seedling establishment (Drivas and Everett, 1988; Whelan et al., 1991). The results from our study also showed that very few tagged seeds removed by rodents were eaten immediately, most being hoarded for later use (Smith and Reichman, 1984; Reichman, 1988; Vander Wall, 1990).

4.5. Cache size

In this study, small rodents made a large number of scattered caches. Cache size ranged from 1 to 3 seeds; most caches contained only one seed, which is indicative of scatter-hoarding (Smith and Reichman, 1984; Vander Wall, 1990). It is generally believed that hoarding strategy is affected by the ability of animals to protect their food resources (Smith and Reichman, 1984; Jiang, 1995; Preston and Jacobs, 2001). When animals can protect their food resources from competitors, a larder hoarding strategy is favoured. If the hoarders have low ability to protect their hoarded food, they will employ a scatter-hoarding strategy, which will avoid catastrophic loss of all hoarded food (MacDonald, 1976). With the coming winter and a poor food supply, competition for limited food resources among individuals becomes intensive, and rodents might adopt a more efficient means of hoarding food, i.e., by putting more seeds in each cache. We observed caches with two and three seeds only in autumn. We presume that several factors, e.g. shorter photoperiod in autumn, have strengthened food-hoarding behaviour of small rodents occurring in temperate region (Shang, 1998).

Acknowledgements

This work was supported by the key projects (FS2000-009, G2000046802) of the Ministry of Science and Technology of the People's Republic of China, and the key project (KSCX2-SW-103) of the Chinese Academy of Sciences. We thank Mr. Wang Fu-Sheng, Mr. Yi Chui-Gui, Dr. Wang Yu-Shan and Dr. Li Hong-Jun for their help in field study.

References

Abbott, H.G., Quink, T.F., 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51, 271–278.

Chen, W., Gao, W., Fu, B.-Q., 2002. Mammalian Fauna of Beijing. Beijing Press, Beijing, pp. 249–254 (in Chinese).

Drivas, E.P., Everett, R.L., 1988. Water relations characteristics of competing single leaf pinyon seedling and sagebrush nurse plants. For. Ecol. Manage. 23, 27–37.

Duncan, R.S., Chapman, C.A., 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecol. Appl. 9 (3), 998–1008.

Forget, P.-M., Vander Wall, S.B., 2001. Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents. Trends Ecol. Evol. 16 (2), 65–67.

Forget, P.-M., Milleron, T., 1991. Evidence for secondary seed dispersal by rodents in Panama. Oecologia 87, 596–599.

Jensen, T.S., Nielson, O.F., 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70, 214–221.

Jiang, Z.-G., 1995. Food hoarding in red squirrels. In: Zhang, J. (Ed.), Studies on Mammal Biology in China. Chinese Forestry Press, Beijing, pp. 185–190 (in Chinese with English abstract).

Kollmann, J., Schill, H.-P., 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio 125, 193–205.

Li, H.-J., 2002. Effect of small rodents on seed regeneration of forest. PhD Dissertation, Graduate School of the Chinese Academy of Sciences, pp. 1–99 (in Chinese with English abstract).

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.

Lima, S.L., 1998. Stress and decision making under the risk of predation: recent development from behavioral, reproductive, and ecological perspectives. Adv. Study Beha. 27, 215–290.

Longland, W.S., Clements, C., 1995. Use of fluorescent pigments in studies of seed caching by rodents. J. Mammal. 76, 1260–1266.

Ma, K.-P., Chen, L.-Z., Yu, S.-L., Huang, J.-H., Gao, X.-M., Liu, C.-R., 1997. The major community types in Dongling mountain region. In: Chen, L.-Z., Huang, J.-H. (Eds.), Structure and Function of Warm Temperature Forest Ecosystem. Science Press, Beijing, pp. 56–75 (in Chinese with English abstract).

MacDonald, D.W., 1976. Food caching by red foxes and other carnivores. Z. Tierpsychol. 42, 170–185.

Morris, D., 1962. The behaviour of the green acouch (*Myoprocta pratti*) with special reference to scatter-hoarding. Proc. Zool. Soc. London 139, 701–732.

Preston, S.D., Jacobs, L.F., 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Beha. Ecology 12, 517–523.

Price, M.V., Waser, N.M., McDonald, S., 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. J. Mammal. 81, 97–106.

Reichman, O.J., 1988. Caching behavior by eastern woodrats, *Neotoma floridana*, in relation to food perishability. Anim. Beha. 36, 1525–1532.

Russell, S.K., Schupp, E.W., 1998. Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). Oikos 81, 434–443.

Shang, Y.-C., 1998. Behavior Ecology. Beijing University Press, Beijing, pp. 50–54.

Smith, C.C., Reichman, O.J., 1984. The evolution of food caching by birds and mammals. Ann. Rev. Ecol. Syst. 15, 329–351.

Sork, V.L., 1984. Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. Ecology 65, 1020–1022.

Vander Wall, S.B., 1990. Food Hoarding in AnimalsUniversity of Chicago Press, Chicago.

Vander Wall, S.B., 1993. Caches 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., 1997. Dispersal of single leaf piñon pine (*Pinus monophylla*) by seed-caching rodents. J. Mammal. 78 (1), 181–191.

Vander Wall, S.B., Joyner, J.W., 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. Can. J. Zool. 76, 154–162.

Vander Wall, S.B., Thayer, T.C., Hodge, J.S., Beck, B.J., Roth, J.K., 2001. Scatter-hoarding behavior of Deer mice (*Peromyscus maniculatus*). West. N. Am. Nat. 61, 109–113.

Whelan, C.J., Willson, M.F., Tuma, C.A., Souza-Pinto, I., 1991. Spatial and temporal patterns of post-dispersal seed predation. Can. J. Bot. 69, 428–436.

Willson, M.F., 1993. Dispersal mode, seed shadows and colonization patterns. Vegetatio 107, 261–280 /108.

Zhang, Z.-B., Wang, F.-S., 2001. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). Acta Ecology Sinica 21 (5), 839–845 (in English with Chinese abstract).

Zhang, Z.-B., Hao, S.-S., Wang, F.-S., Wang, S.-Q., Meng, Z.-B., Wang, Z.-W., 1998. Influence of rodents on generation of forests in the mountain region near Beijing. Bull. Russ. Acad. Sci. 4, 467–470.