

# Rodent-favored cache sites do not favor seedling establishment of shade-intolerant wild apricot (*Prunus armeniaca* Linn.) in northern China

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**Abstract** Seed dispersal by scatter hoarders is widely assumed to involve directed dispersal, in which microhabitats selected for caching also benefit seedling establishment and growth. However, in many systems, this may not be true if animal-favored cache sites do not match the safe sites for plants, or if cache sites benefit the plant in one life stage and not another. Here, we investigated whether cache sites selected by rodents are favorable for seedling establishment and growth of shade-intolerant wild apricot (*Prunus armeniaca* Linn.) in northern China. We tracked tagged seeds and compared the germination and growth of seedlings from rodent-cached seeds with that of naturally established seedlings in a secondary forest and shrubland stand. Rodents preferred to cache seeds under shrubs with medium canopy cover

(31–60 %) in litter substrate in the secondary forest, and under shrubs with high canopy cover (>60 %) in soil or litter substrate in the shrubland stand, neither of which conveyed an advantage for seedling establishment. Although fewer caches were made along shrub edges, or under low canopy cover ( $\leq 30$  %) in the secondary forest, or along shrub edges, open areas of grass, or under low canopy cover in the shrubland stand, these cache sites consistently contributed to higher survival rates. The microhabitats of grass, soil, or low canopy cover significantly promoted the emergence, survival, and growth of naturally established seedlings. Our results are best explained by the conflicting demands of rodents for caching seeds in more secure sites and *P. armeniaca*'s high-light requirements for seedling recruitment. We argue that the relationship between favored cache sites for seed hoarders and safe sites for plants will often not match but may still allow a reasonable rate of establishment and regeneration.

**Keywords** *Prunus armeniaca* Linn. · Safe site · Scatter hoarding · Seed dispersal · Seed survival · Seedling establishment · Seedling growth

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## Introduction

The dispersal of seeds by seed-caching animals is widely recognized as a key determinant of the spatial structure and dynamics of plant populations and

communities (McAlpine and Jesson 2008; Vander Wall 2010; Carlo et al. 2011). Many vertebrate agents of seed dispersal, such as corvids and rodents, play a significant role in the regeneration of plants by hoarding seeds in microhabitats that are coincidentally favorable to seedling establishment and growth, and then subsequently failing to recover a portion of these seeds (Howe and Smallwood 1982; Chimera and Drake 2011). Safe sites for seedling establishment are typically associated with specific microhabitats (e.g., vegetation type, substrate, and levels of canopy cover) that affect the level of light, moisture and temperature required for seed germination and growth, thereby providing suitable refuges for new seedlings (Wenny and Levey 1998; Briggs et al. 2009). Consequently, patterns of cache-site selection by seed-hoarding animals may directly influence plant fitness and the spatial patterns of plant populations (Howe and Smallwood 1982; Howe and Miriti 2004; Spiegel and Nathan 2010).

Several studies have shown that animals cache seeds nonrandomly across microhabitats (Nathan and Muller-Landau 2000; Zhang et al. 2008; Green et al. 2009), but whether animal-preferred cache sites facilitate long-term seedling establishment and growth is poorly studied (but see Briggs et al. 2009). Those studies that have tracked animal dispersed seeds over relatively short periods (<2 years) have seen varied outcomes. For example, in northern Arizona, brush mice (*Peromyscus boylii*) and pinyon mice (*P. trueii*) preferred to hoard pinyon pine (*Pinus edulis* Engel.) seeds in small-particle soils near rocks, which benefited the plant by increasing seed survival, seedling establishment, and growth (Pearson and Theimer 2004). But in temperate forests in central Japan and north China, survival and establishment of cached acorns (*Quercus* spp.) in rodent-favored microhabitats (e.g., under dense shrubs and trees) was consistently lower than in other microhabitats, such as forest edges and gaps (Iida 2006; Zhang et al. 2008). In a longer study (8 years), Briggs et al. (2009) found rodents cached Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) seeds nonrandomly with respect to available microhabitats, and seeds cached in some microhabitats showed higher rates of germination and seedling emergence than those in other microhabitats; yet naturally occurring older seedlings were often found in more open microhabitats.

Perhaps these varied results across systems reflect variation in the stages of the coevolution of the plant–

hoarder relationship. However, they also suggest a convenient framework for evaluating the outcome of ecological interactions. We suggest that such a relationship may vary across a continuum in which: at one end, conditions of the cache directly “match” those needed for plant establishment and growth (i.e., complete match or directed dispersal, Wenny and Levey 1998), and at the other end, cache sites are unsuitable for plant establishment (i.e., complete mismatch).

To our knowledge, most studies on the effects of animal-mediated seed dispersal on plant regeneration have been done by tracking seed deposition patterns (via caches) within variable microhabitats and then estimating initial patterns of seedling establishment and survival (e.g., Hoshizaki et al. 1999; Iida 2006; Pearson and Theimer 2004; McAlpine and Jesson 2008; Klinger and Rejmánek 2010). Unfortunately, little appears to be known about the long-term success of cached seeds and seedlings among microhabitats favored by hoarding animals, and whether or not the microhabitats selected by caching animals are indeed favorable for each of the life stages of seed and seedling development (but see Briggs et al. 2009). For example, cache sites offering favorable conditions for germination may not always be best for later stages of establishment and growth (Schupp 2007; Spiegel and Nathan 2012). Thus it is essential to evaluate the long-term effects of hoarding decisions on plant establishment and growth. Here, we attempt such a study to understand how hoarding decisions influence dispersal, establishment and growth of a common rodent-dispersed plant species in northern China.

Wild apricot (*Prunus armeniaca* Linn.) is a widely distributed, shade-intolerant, deciduous tree or shrub that inhabits forests and shrublands of northern China (Lu et al. 2005). Following seedfall, its seeds undergo secondary dispersal exclusively by rodents due to their hard woody endocarp, which prevents consumption by other animals (e.g., birds, insects; Lu and Zhang 2004). Previous research has shown that *P. armeniaca* seeds may be nonrandomly hoarded in certain microhabitats by small rodents (Lu and Zhang 2004; Li and Zhang 2007), but we know little about the subsequent effects of the microhabitats of caches on seed survival and seedling establishment and growth.

We tracked *P. armeniaca* seeds in both a shrubland and a secondary forest during a period of natural seedfall and seed dispersal (July) by recording the

microhabitat characteristics selected by small rodents for hoarding, and by tracking cache survival until the following spring. We also recorded all seedlings from rodent-made caches and their survival for the following three years. In addition, we compared the microhabitats of naturally established seedlings (1–4 years old) of *P. armeniaca* (i.e., safe sites for seeds and seedlings) with those of rodent cache sites to determine the extent to which there was a “match” or “mismatch” between the two. Our objectives were to determine: (1) the microhabitats of the cache sites favored by small rodents when hoarding *P. armeniaca* seeds; (2) the safe sites for seedling establishment and growth of *P. armeniaca*; and (3) if the microhabitats of cache sites favored by seed-hoarding rodents match, or fail to match, those required for seedling establishment and growth of *P. armeniaca*.

## Materials and methods

### Study area

This study was conducted at the Liyuanling field station in the Donglingshan Mountains, northern China (40°00'N, 115°30'E; 1,100 m a.s.l.; 120 km northwest of Beijing city). The area has a temperate continental monsoon climate with 600 mm of annual precipitation and 6.5 °C of average annual temperature. Shrublands, secondary forests, and abandoned farmlands are the principle habitats in the region as it gradually undergoes natural secondary succession from cultivation and grazing. In the secondary forests, Liaodong oak (*Quercus liaotungensis* Koidz), *P. armeniaca*, wild walnut (*Juglans mandshurica* Maxim.), elm (*Ulmus laciniata* Trautv.), larch (*Larix principis-rupprechtii* Mayr), and wild peach (*Amygdalus davidiana* Carr.) are the dominant plants; dwarf shrubs and annual herbs comprise the layers below the canopy; and litter and bare ground are present on the surface layer. In the shrublands, young *Q. liaotungensis*, *P. armeniaca*, *U. laciniata*, and chastetree (*Vitex negundo* Linn.) are the primary plant species; dwarf shrubs and herbs occur under the shrub cover; and the ground surface is comprised of litter and bare ground. Dominant plant species in the abandoned farmlands include annual herbs, younger stems of *P. armeniaca* and *V. negundo*, and some sparsely distributed cultivated trees (e.g., walnut, *J. regia*). Chinese white-bellied rats (*Niviventer confucianus*), Korean

field mice (*Apodemus peninsulae*) and Père David's rock squirrels (*Sciurotamias davidianus*) are the most common rodent species, whereas striped field mice (*A. agrarius*), greater long-tailed hamsters (*Tscherskia triton*), and Siberian chipmunks (*Tamias sibiricus*) are also found across the study area (Zhang and Zhang 2008). All of these species engage in scatter and/or larder hoarding of seeds, and are responsible for the majority of seed consumption and dispersal of the trees listed above (Zhang 2007).

### Focal plant and seed-marking

*Prunus armeniaca* trees and shrubs, common in northern China, are widely distributed in the study area. The fruit of *P. armeniaca* is a drupe. After maturation in July, the fleshy layer (mesocarp) opens and the dispersal unit, comprised of a single seed enclosed in a hard endocarp (hereafter the seed), falls to the ground. Seedlings often emerge during the next spring (April–May). Due to the high crude fat content (53.1 %) and relatively high caloric value (25.5 kJ/g) of their kernels, medium size ( $1.2 \pm 0.2$  g mass;  $22.1 \pm 1.6$  mm long,  $9.8 \pm 0.8$  mm wide, including endocarp, mean  $\pm$  SD,  $N = 50$ ) and moderately hard woody endocarp ( $1.1 \pm 0.2$  mm thickness), fresh *P. armeniaca* seeds are favored for consumption and hoarding by rodents (Zhang and Zhang 2008). *P. armeniaca* seeds are shown to be dispersed strictly by rodent species in today's forests and rodents deposit a single seed per cache (Lu and Zhang 2004).

At the beginning of seedfall and the seed dispersal period (beginning of July) in 2007 and 2008, fresh and intact seeds were collected from *P. armeniaca* outside the experimental plots (>500 m) and kept in a dry and ventilated storage area to prevent rotting and mildew growth. All experimental seeds were marked following the tin-tag method to facilitate rapid relocation: a 0.5 mm hole was drilled into the endocarp of each seed and a unique coded tin-tag (30  $\times$  10 mm, 0.1 g) was tied to each seed with a 3-cm piece of fine steel wire (Zhang and Wang 2001). The wire tags do not appear to affect dispersal by rodents (Xiao et al. 2006).

We selected two experimental plots (3 ha areas separated by 300 m) for seed placement: one in a shrubland and the other in a secondary forest. *P. armeniaca* trees/shrubs were common at both plots. The secondary forest plot was located on a northeast-facing slope of 45–65° and dominated by trees

of *Q. liaotungensis*, *P. armeniaca*, and *L. principis-rupprechtii* ( $8.2 \pm 3.2$  m (mean  $\pm$  SD,  $N = 100$ ) in height, with  $>80$  % canopy cover; Zhang et al. 2008). The herbaceous and surface layers below the forest canopy were occupied by annual herbs, young trees, shrubs, litter, and bare ground. Shrubland and abandoned farmland communities are located at the foot of the slope. The shrubland plot was located on a southeast-facing slope of  $30^\circ$ – $45^\circ$  and dominated by *U. laciniata*, *P. armeniaca*, and *Q. liaotungensis* shrubs ( $2.2 \pm 1.7$  m ( $N = 100$ ) in height, with 65 % shrub cover; Zhang et al. 2008). The herbaceous and surface layers below the shrub canopy were covered by grasses, young shrubs, and litter.

### Seed placement

Seed placement was conducted during the seed dispersal period of *P. armeniaca* (5 Jul.–4 Aug. 2007 and 8 Jul.–7 Aug. 2008). Within each experimental plot in the forest and shrubland, five seed stations ( $0.5 \text{ m}^2$ , 30 m apart) were established along each of three parallel transects (150 m long and 30 m apart) ( $N = 3 \times 5 = 15$ ). Thirty tagged seeds were placed on the ground at each station. A total of 1,800 tagged seeds were released over the 2 years. All seed stations were checked every day for 30 successive days until only a few seeds remained at the source. The individually cached seeds (buried in soil, litter, or grass) were relocated within 50 m of each station by visually searching for tags. When located, a cache was marked using a uniquely coded wooden stick placed at least 30 cm away from the cache to minimize any visual cues that rodents might use for cache retrieval. The microhabitat (vegetation type, substrate, and level of canopy cover) at each cache site were recorded (also see Li and Zhang 2003).

The vegetation type of each cache site was assigned to one of the four categories following Li and Zhang (2003): (1) under shrub, indicating the seed was buried under dense shrub cover; (2) shrub edge, when the seed was buried at the edge of shrub cover, near open areas where light penetrated the forest floor; (3) bare ground, when the cached seed was buried in open ground outside any cover; and (4) open grassland, when the seed was buried in open grassland without shrub cover. Cache substrate, the materials directly covering seeds, were classified as: (1) soil only, (2) litter, when the cached seed was covered with leaves or twigs; and (3) grass, when the cache was covered by

grass only. Canopy cover by trees or high shrubs ( $\geq 1.5$  m) over the cache sites were measured using a spherical densiometer and classified into one of three categories: (1) low,  $\leq 30$  %, (2) medium, 31–60 %, and (3) high, 61–100 %. The proportions for each category of vegetation type, substrate and canopy cover of cache sites at each of the 15 seed stations were used to determine patterns of cache placement (observed use) for each variable ( $\pm$ SE,  $N = 15$ ) in both the shrubland and secondary forest plots. To calculate expected measures of each vegetation type, substrate and level of canopy cover, we estimated the percentage of each in a random  $5 \times 5$  m quadrat, 2 m from each seed station (also see Lu and Zhang 2004).

Following scatter-hoarding of seeds by rodents, caches, which consisted of a single seed, were visited every day over a 30-day period, and again the following spring (May). Cache survival times were recorded as  $\leq 10$  days, 11–20 days, 21–30 days,  $>30$  days or next spring (NS). The fates of all seedlings established from rodent caches were tracked for three additional years.

### Natural patterns of seedling establishment and growth

To compare microhabitat characteristics of successful *P. armeniaca* seedlings (i.e., safe sites) with those of cache sites selected by rodents, five belt transects (200 m long, 10 m wide, 100 m apart) were used to measure the microhabitats and growth of naturally established seedlings in secondary forests, shrublands as well as abandoned farmlands where seedlings also establish (15 transects in total). For each of the 409 *P. armeniaca* seedlings (1–4-years old) found on these transects, in July 2011, we determined the vegetation type, substrate and canopy cover associated with each naturally established seedling following procedures above. The frequencies of seedlings in each category were used to estimate the observed frequencies for these naturally occurring seedlings. In addition, we measured the basal diameter, height, and leaf number of each seedling to evaluate seedling growth and performance. Along each transect, we used five regularly spaced quadrats ( $5 \times 5$  m, 50 m apart,  $5 \times 15 = 75$  quadrats in total) to measure the availability of each microhabitat in the environment to compare with the same characteristics associated with these naturally established seedlings.

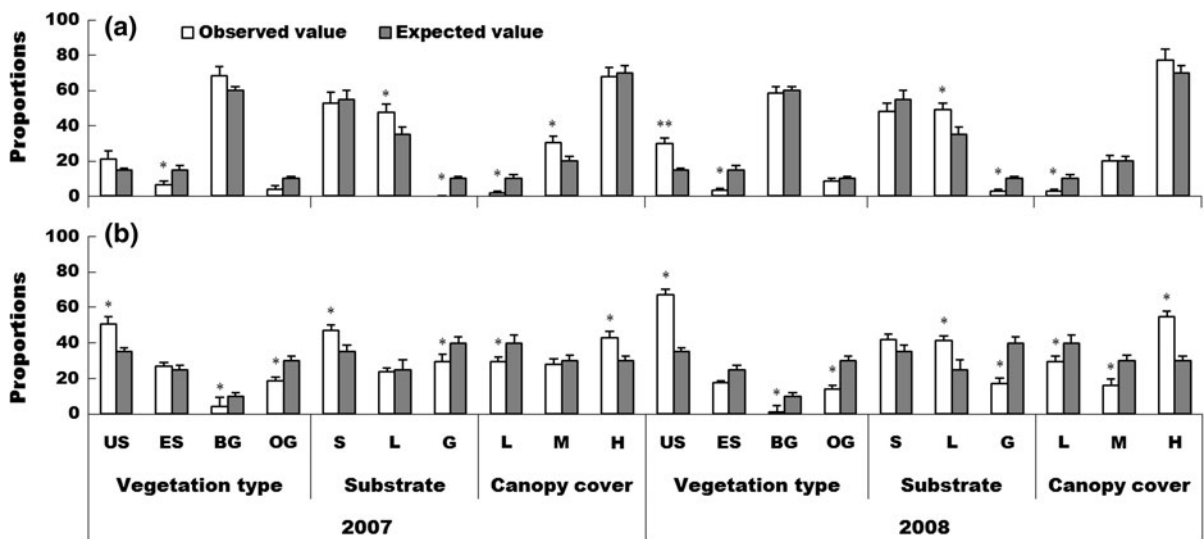
Statistical analyses

Data were analyzed with SPSS for Windows v16.0 (SPSS Inc. 2008). Data were first tested for normality using the Shapiro–Wilk’s test and, if significantly different from normality, log-transformed to achieve normality. Independent-samples *t* tests were used to test for differences ( $P < 0.05$ ) between observed and expected measures of each category of vegetation type, substrate, and level of canopy cover for both cache sites selected by rodents, and the distribution of naturally established seedlings. We used life-table analyses to calculate median survival times of caches for each category of vegetation type, substrate, and canopy cover by plot and year. Cox regression was used to determine the main effects of plot, year and their interactions on cache survival, as well as differences in cache survival among vegetation type, substrate, and canopy cover. One-way ANOVA was used to determine differences in seedling distributions as well as differences in the basal diameter, height, and leaf number of stems of each age class (1–4-years old) across each vegetation type, substrate or level of canopy cover. We used a GLM-multivariate test

(MANOVA) to determine main effects of age, vegetation type, substrate, canopy cover (fixed factors) and their interactions on the basal diameter, height, and leaf number (dependent variables) of the naturally established seedlings. For both one-way ANOVAs and MANOVAs LSD was used to make pairwise comparisons.

Results

Of the 1,800 seeds presented, 592 primary caches, each containing a single seed, were recorded across both plots during the 2-year study. In the secondary forest plot, rodents cached significantly more often under shrubs (2008), in the litter substrate (2007, 2008), or under medium canopy cover (2007) ( $P < 0.05$ , *T* test, Fig. 1a). In contrast, shrub edges (2007, 2008), grass substrate (2007, 2008), or low canopy cover (2007, 2008) were used significantly less often by rodents for caching ( $P < 0.05$ , *T* test, Fig. 1a). In the shrubland plot, seeds were cached more often under shrubs (2007, 2008), in soil (2007) and litter (2008) substrate, or under high canopy cover



**Fig. 1** Comparisons of the observed distribution of wild apricot (*Prunus armeniaca*) seeds cached by small rodents across categories of vegetation type, substrate or levels of canopy cover and the expected distribution of the same measures by plot and year in the secondary forest plot (a) and the shrubland plot (b). All data are proportions (mean ± SE, *N* = 15). Vegetation type includes: *US* under shrub, *ES* shrub edge, *BG* bare ground, *OG*

open grassland. Substrate includes: *S* soil, *L* litter, *G* grass. Canopy cover indicates estimate of percent coverage of high shrubs ( $\geq 1.5$  m tall) and/or trees over the cache sites, and includes *L* low,  $\leq 30$  %, *M* medium, 31–60 % and *H* high, 61–100 %. \* $P < 0.05$ , and \*\* $P < 0.01$  following independent-samples *T* test



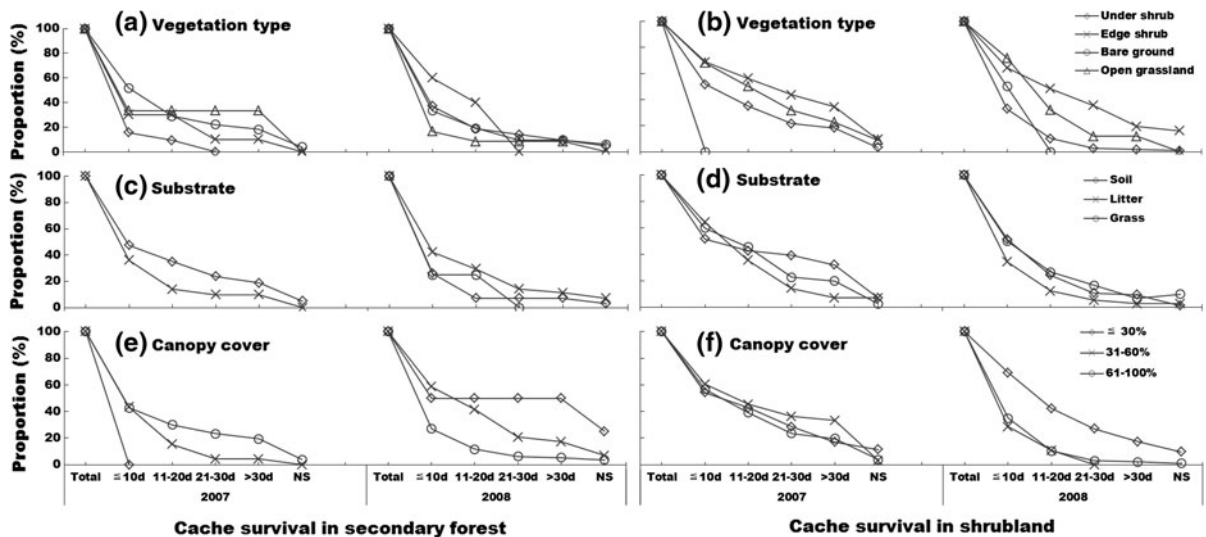
(2007, 2008), whereas rodents cached significantly less often in bare ground (2007, 2008) and open grassland (2007, 2008), grass substrate (2007, 2008), or under low (2007, 2008) and medium canopy cover (2008) ( $P < 0.05$ , Fig. 1b). Overall, small rodent preferred to cache seeds under shrubs, in soil or litter substrate, under medium to high canopy cover ( $>30\%$ ).

Most caches (42.9–66.0 %) were removed within 10 days, whereas some caches survived more than 30 days (5.6–22.7 %); fewer survived until the following spring (2.6–5.9 %) (Appendix, Fig. 2). A significant effect of plot on cache survival was observed (Wald = 6.215, df = 1,  $P = 0.013$ , Cox regression). Cached seeds in the shrubland plot disappeared more slowly and survived at a higher rate than those in the secondary forest plot (Fig. 2). Cache survival rate was also significantly affected by vegetation type (Wald = 3.866, df = 1,  $P = 0.049$ , Cox regression), substrate (Wald = 4.934, df = 1,  $P = 0.026$ ), and canopy cover (Wald = 4.812, df = 1,  $P = 0.034$ ). Significant interactions between vegetation type and substrate (Wald = 3.981, df = 1,  $P = 0.047$ ), and canopy cover and substrate (Wald = 6.831, df = 1,  $P = 0.009$ ) were also detected. In the secondary forest plot, caches made in bare ground (2007, 2008) and open grassland (2007), substrate of soil (2007, 2008) and

litter (2008), or medium canopy cover (2007, 2008) showed high survival rates (Appendix, Fig. 2a, c, e). In the shrubland plot, survival rates were highest in the shrub edge (2007, 2008) and open grassland vegetation types (2007), and in the soil (2007), grass (2008) and litter substrate (2007, 2008), or under low canopy cover (2007, 2008) (Appendix 1, Fig. 2b, d, f).

Only three seedlings (one in 2007 and two in 2008) established from rodent caches in the secondary forest plot. Similarly, 11 seedlings (five in 2007 and six in 2008) established in the shrubland plot. Caches along the shrub edge, in soil substrate, or under low canopy cover showed the highest establishment probability (Appendix). Only two seedlings in the shrubland plot survived beyond 3 years: one grew at shrub edge with soil substrate and 40 % canopy cover; the other grew at shrub edge with litter substrate and 15 % canopy cover (Appendix).

We located and measured 409 naturally established *P. armeniaca* seedlings, ranging in age from 1- to 4-years old. Compared with patterns of availability, seedlings of *P. armeniaca* were found significantly more often in open grassland, with soil substrate, or under low canopy cover, whereas fewer were established under shrubs and at shrub edges, in litter and grass substrate, or under high canopy cover ( $P < 0.05$ , *T* test, Fig. 3a). Seedling numbers decreased with

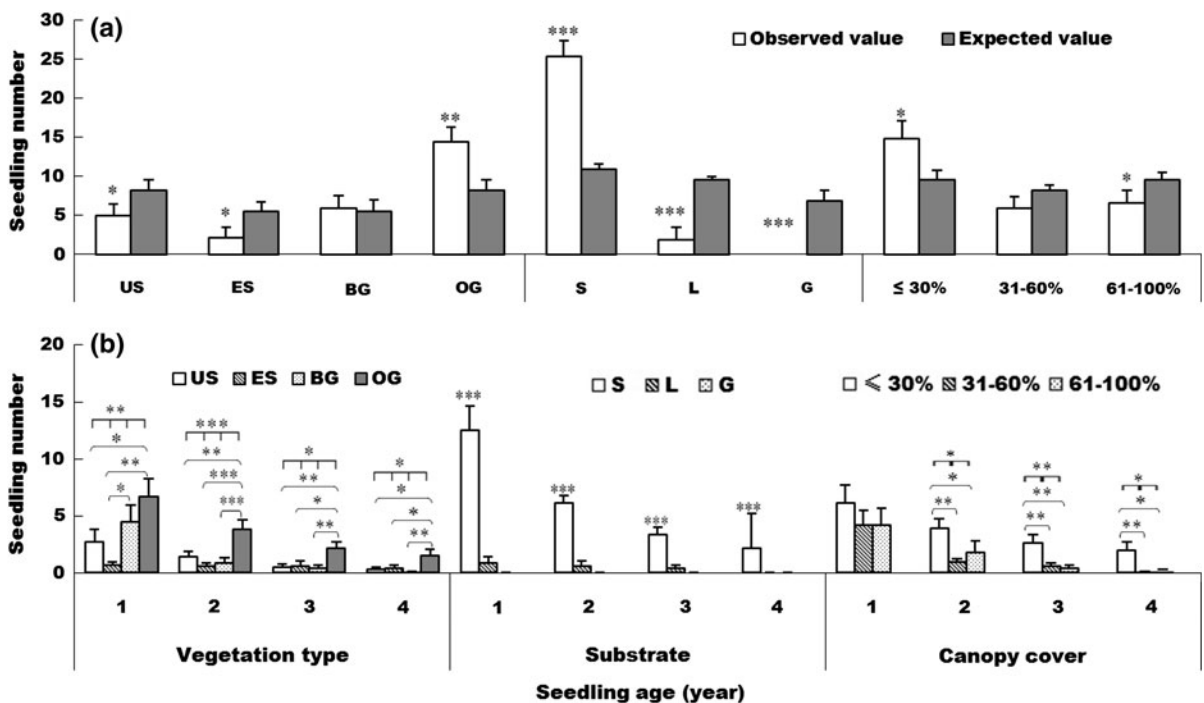


**Fig. 2** Cache survival dynamics of wild apricot (*Prunus armeniaca*) seeds hoarded by small rodents among different vegetation type (a, b), substrate (c, d) or levels of canopy cover (e, f) by plots and years. All data are proportions of total seeds. NS next spring. Vegetation type includes: US under shrub, ES

shrub edge, BG bare ground, OG open grassland. Substrate includes: S soil, L litter, G grass. Canopy cover indicates estimates of percent coverage of high shrubs ( $\geq 1.5$  m tall) and/or trees over the seedlings

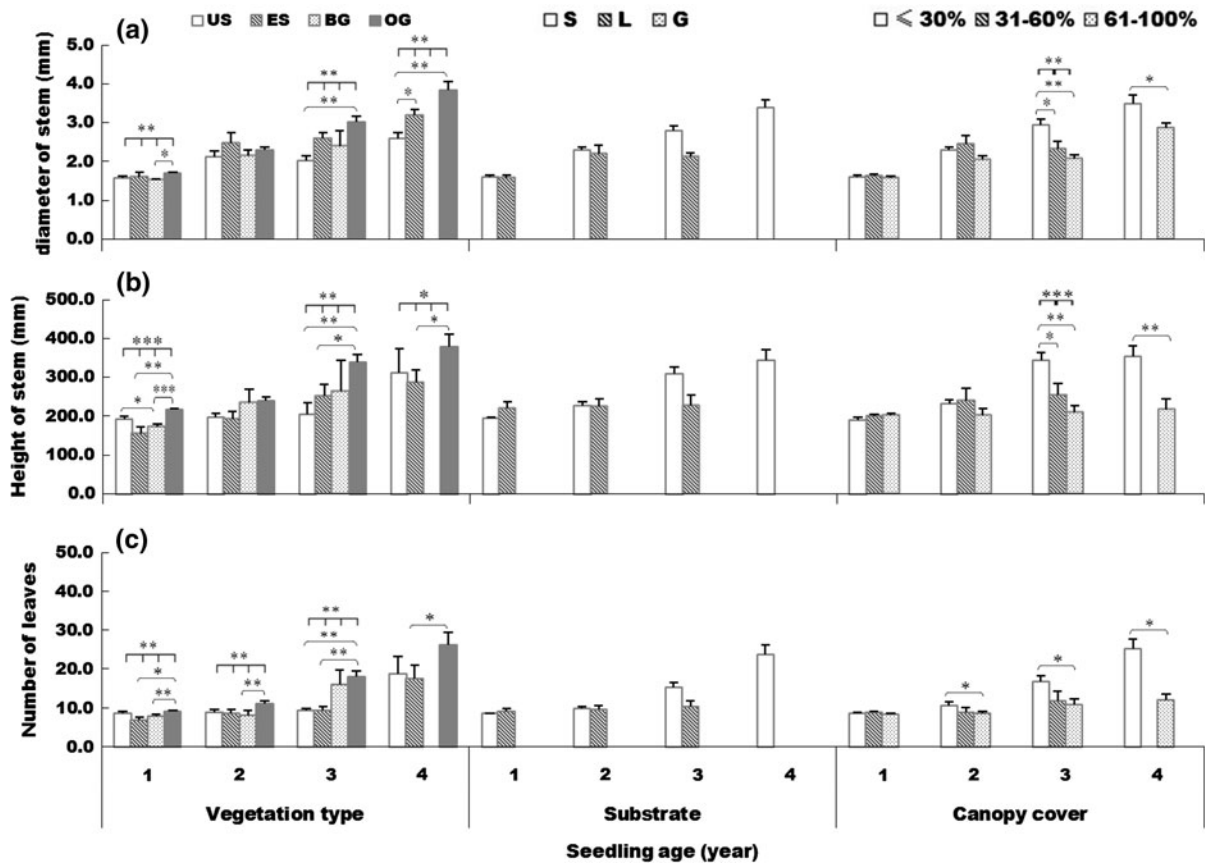
seedling age in all vegetation types, substrate, and levels of canopy cover (Fig. 3b). The distribution of 1-year seedlings differed significantly across vegetation types ( $F_{3,56} = 4.738, P = 0.005$ , one-way ANOVA) and substrate ( $F_{2,42} = 30.335, P < 0.001$ ). More 1-year seedlings were found in bare ground and open grassland, or soil substrate ( $P < 0.05$ , LSD pairwise comparisons) (Fig. 3b). We detected significant effects of vegetation type (2-year:  $F_{3,56} = 7.151, P < 0.001$ ; 3-year:  $F_{3,56} = 4.005, P = 0.012$ ; 4-year:  $F_{3,56} = 3.256, P = 0.038$ ), substrate (2-year:  $F_{2,42} = 56.564, P < 0.001$ ; 3-year:  $F_{2,42} = 18.158, P < 0.001$ ; 4-year:  $F_{2,42} = 8.041, P = 0.001$ ) and canopy cover (2-yr:  $F_{2,42} = 4.054, P = 0.025$ ; 3-yr:  $F_{2,42} = 6.814, P = 0.003$ ; 4-year:  $F_{2,42} = 4.871, P = 0.013$ ) on the distributions of 2- to 4-year seedlings. More 2- to 4-year seedlings grew in the open grassland, soil substrate, or under low canopy cover ( $P < 0.05$ ) (Fig. 3b). Overall those seedlings in open grassland, soil substrate, or under low canopy cover showed higher rates of survival at 4 years of age (Fig. 3b).

Results of the MANOVA revealed a significant effect of age ( $F_{3,357} = 16.790, P < 0.001$ ), vegetation type ( $F_{3,357} = 4.657, P = 0.003$ ), canopy cover ( $F_{3,356} = 3.455, P = 0.017$ ) and interactions between age and vegetation type ( $F_{8,357} = 3.301, P = 0.001$ ), age and canopy cover ( $F_{5,357} = 7.929, P < 0.001$ ), age, vegetation type and canopy ( $F_{10,357} = 1.920, P = 0.041$ ) on seedling growth. Overall, older seedlings in open grassland with lower canopy cover grew best. The basal stem diameter was significantly affected by age ( $F_{3,357} = 15.449, P < 0.001$ ) with significant interactions occurring between age and vegetation type ( $F_{8,357} = 2.817, P = 0.005$ ), and age and canopy cover ( $F_{5,357} = 2.409, P = 0.036$ ). The basal stem diameter of the 3- and 4-year seedlings was greatest among those in open grassland or under low canopy cover ( $P < 0.05$ , LSD pairwise comparisons; Fig. 4a). Stem height was significantly affected by age ( $F_{3,357} = 5.237, P = 0.002$ ), and vegetation type ( $F_{3,357} = 4.499, P = 0.004$ ) with significant interactions occurring between age and vegetation type



**Fig. 3** Distribution of naturally established seedlings of wild apricot (*Prunus armeniaca*) across vegetation type, substrate or levels of canopy cover. Shown are observed and expected frequencies (a) across seedling ages (b) within each category of vegetation type, substrate, or level of canopy cover. All data are seedling numbers (mean ± SE,  $N = 15$ ). Vegetation type includes:

US under shrub, ES shrub edge, BG bare ground, OG open grassland. Substrate includes: S soil, L litter, G grass. Canopy cover indicates estimates of percent coverage of high shrubs ( $\geq 1.5$  m tall) and/or trees over the seedlings. \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$  based on independent-samples *T* test (a) and one-way ANOVA (b)



**Fig. 4** Comparisons of basal diameter of stems (a), height of stems (b), and number of leaves (c) of wild apricot (*Prunus armeniaca*) seedlings in each age group (1–4 years) among different categories of vegetation type, substrate, or levels of canopy cover. All data are means ( $\pm$ SE,  $N = 219, 101, 56, 33$  for 1- to 4-year-old seedlings). Vegetation type includes: *US*

under shrub, *ES* shrub edge, *BG* bare ground, *OG* open grassland. Substrate includes: *S* soil, *L* litter, *G* grass. Levels of canopy cover indicate estimates of percent coverage of the canopies of high shrubs ( $\geq 1.5$  m tall) and/or trees over the seedlings. \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$  based on one-way ANOVA

( $F_{8,357} = 2.727$ ,  $P = 0.006$ ), age and canopy cover ( $F_{5,357} = 7.683$ ,  $P < 0.001$ ), and age, vegetation type and canopy cover ( $F_{10,357} = 1.879$ ,  $P = 0.047$ ). The 3- and 4-year seedlings found in the open grassland and under low canopy cover had significantly taller stems than those observed elsewhere ( $P < 0.05$ ; Fig. 4b). Number of leaves per stem was significantly affected by age ( $F_{3,357} = 10.942$ ,  $P < 0.001$ ) and canopy cover ( $F_{2,357} = 3.156$ ,  $P = 0.044$ ) with the two variables also showing a significant interaction ( $F_{5,357} = 3.985$ ,  $P = 0.002$ ). The 3- and 4-year seedlings growing under low canopy cover had significantly more leaves than seedlings found under in other conditions ( $P < 0.05$ ) as did 2-year seedlings growing in open grassland or under low canopy cover ( $P < 0.05$ ; Fig. 4). The 1-year seedlings differed

across vegetation types with respect to stem basal diameter ( $F_{3,215} = 4.220$ ,  $P = 0.006$ ), stem height ( $F_{3,215} = 12.513$ ,  $P < 0.001$ ) and number of leaves ( $F_{3,215} = 3.952$ ,  $P = 0.009$ ); those established in open grassland and under shrubs had larger and taller stems and more leaves ( $P < 0.05$ , LSD pairwise comparisons; Fig. 4). Overall, the open grassland, soil substrate and low canopy cover were most suitable for the emergence, survival and growth of *P. armeniaca* seedlings (Figs. 3, 4).

## Discussion

Our results indicate a general “mismatch” between the cache sites favored by rodents and the safe sites



suitable for seedling establishment and growth of *P. armeniaca*. We found rodents cached *P. armeniaca* seeds nonrandomly with respect to vegetation types, substrate and canopy cover. Most, but not all, of these cache characteristics did not favor subsequent seedling establishment. Cache survival and seedling establishment in these rodent-favored hoarding microhabitats were not significantly higher than for other microhabitats, and, although some seedlings (1–2-years old) were able to establish in the microhabitats where rodents hoarded seeds, few survived beyond this age. Moreover, seedlings growing in microhabitats favored for caching by rodents (e.g., under shrub, high canopy cover) were shorter and had a smaller basal stem diameter than seedlings in other microhabitats.

Our results are consistent with observations of some studies (e.g., Hoshizaki et al. 1999; Zhang et al. 2008; Spiegel and Nathan 2012) but not others in which it has been shown that the movement of seeds by rodents and birds can result in directed dispersal (Wenny and Levey 1998; Wenny 2001; Iida 2006; Briggs et al. 2009; Green et al. 2009). For example, yellow-pine chipmunks (*Tamias amoenus*) preferred to cache *P. jeffreyi* seeds in microhabitats that were favorable for seedling establishment and growth and avoided hoarding seeds in sites where seedlings typically failed (Briggs et al. 2009). Thus, these various results fall along a match–mismatch continuum.

The apparent “mismatch” that we observe between the characteristics of cache sites selected by rodents and the safe sites for seedling of *P. armeniaca*, a shade-intolerant species, may result from the rodents’ preferences for dense cover when caching. This may be due to the natural habitat preferences of the rodents, or alternatively, to higher predation risks outside of cover. The hard woody endocarp of *P. armeniaca* increases rodent handling time which would further increase predation risks if seeds were recovered and eaten in open microhabitats. In some systems, however, similar well-protected cache sites may also represent safe sites for shade-tolerant plants (e.g., Briggs et al. 2009) for which establishment and regeneration depends on such shade tolerance (Kitajima 1994).

It is not surprising that small rodents hoard seeds nonrandomly (Iida 2006; Zhang et al. 2008). Rodents are faced with a distinct trade-off between energy investment and rewards (return rates) when hoarding (Vander Wall 1990). Seed-hoarding rodents employ a

variety of tactics to harvest seeds, locate favorable cache sites, minimize cache losses, enhance retrieval rates and decrease the risk of predation (Vander Wall and Jenkins 2003). How hoarders employ various strategies to balance rewards and alleviate predation risk in differing microhabitats requires further investigation.

Based on our assessment of the natural distribution of *P. armeniaca* seedlings, it appears this species establishes and grows best in open grassland with a substantial soil substrate, confirming the importance of soil and light on this process. Most caches were located under shrubs in shrublands or on bare ground in forests with extensive canopy cover. Areas of high shrub and tree density increase the probability of cache loss by providing ideal shelter for seed predators (Nathan and Muller-Landau 2000), and possibly other agents of density-dependent mortality (Donohue 1997; Nathan and Muller-Landau 2000; Visser et al. 2011). In our system, however, it does appear that when seeds are occasionally dispersed to more open sites, these seeds have a disproportionately higher rate of establishment and growth. Perhaps this higher success rate for a small number of seeds translates into a consistent rate of suitable establishment.

We also found, however, that different microhabitats appear to be favorable for *P. armeniaca* seedlings at different life stages. The favorable places for seeds are not always best for seedlings and/or saplings; consequently, animal-generated dispersal patterns may differ from the final spatial pattern of recruitment (Rey and Alcántara 2000). In our study, seedlings that established in open grassland, in soil substrate or with low canopy cover experienced better long-term survival. These results confirm that the level of light is a limiting factor for *P. armeniaca* seedling growth, a shade-intolerant species found on the southern slopes of mountains (Lu et al. 2005). Similarly, Briggs et al. (2009) found that seedlings in soil and under shrubs are more likely to survive their first year, but not thereafter; those that establish in open areas with light-litter substrate experienced higher long-term survival. Abiotic factors such as light, temperature, substrate, moisture, and microtopography can have very different effects on seed germination, seedling establishment and seedling growth at different ages (Garcia et al. 2002). Thus the “match” or “mismatch” between rodent-favored cache sites and safe sites for seedling establishment should not be determined simply by

patterns of germination and early seedling recruitment but also by long-term seedling survival and growth.

Although the primary cache sites of rodents did not match the safe sites for seedling establishment of *P. armeniaca*, rodents still perform important roles in the dispersal of *P. armeniaca* by depositing a proportion of seeds in microhabitats favorable for establishment (e.g., open grass and shrub edges) (also see Zhang 2007). One possible reason for this is that such safe sites may reduce pilfering rates in heavy cover where rodent activity is likely higher. Primary caches of *P. armeniaca* may sometimes be re-cached in more open areas to reduce cache pilferage (Zhang 2007). Eastern gray squirrels (*Sciurus carolinensis*) in deciduous forests of North America (Steele et al., in prep) and small rodents in scrub oak forests of Spain (Muñoz and Bonal 2011) selectively cache seeds outside cover to potentially reduce cache pilferage. As Muñoz and Bonal (2011) note, sites best for caching, where pilferage risks are lower, may also represent the same sites suitable for seedling establishment and growth; in their study, this resulted in the caching of 77 % of seeds in such sites.

We suggest that seedling survival in our system and many others is likely tied to the integrative effects of microhabitats on both the cache management process and long-term seedling success. Only rarely will these two factors coincide in such a way to result in successful establishment and long-term seedling survival and growth (i.e., directed dispersal). Future studies should consider the relative match between the microhabitats of cache sites and that required for all stages of plant recruitment. Such systematic evaluations represent a consistent approach for quantifying and comparing the efficacy of animal-mediated dispersal across systems.

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## Appendix

See Table 1.

**Table 1** Distributions of rodent-made caches of wild apricot (*Prunus armeniaca*) seeds, cache survival patterns, and seedling establishment and survival across different categories of vegetation type, substrate or levels of canopy cover

Plots	Years	Cache sites	Vegetation type	Total caches	Cache survival					Seedlings			
					≤10 days	11–20 days	21–30 days	>30 days	NS	MST (days)	Total	Survival (year)	
Secondary forest	2007	Vegetation type	Under shrub	32 (21.5)	27 (84.4)	2 (6.3)	3 (9.4)	0	0	0	6.3	0	0
			Shrub edge	10 (6.6)	7 (70.0)	0	2 (30.0)	1 (10.0)	0	0	8.5	0	0
			Bare ground	104 (68.4)	50 (48.1)	24 (23.1)	7 (6.7)	19 (18.3)	4 (3.8)	10.3	1 (1.0)	1	0
			Open Grassland	6 (3.9)	4 (66.7)	0	0	2 (33.3)	0	10	0	0	0
			Soil	80 (52.6)	42 (52.5)	10 (12.5)	9 (11.3)	15 (18.8)	4 (5.0)	10.7	1 (1.3)	1	0
			Litter	72 (47.4)	46 (63.9)	16 (22.2)	3 (4.2)	7 (9.7)	0	8	0	0	0
			Grass	0	0	0	0	0	0	–	0	0	0
			Canopy cover (%) ≤30	3 (2.0)	3 (100.0)	0	0	0	0	–	0	0	0
			31–60	46 (30.3)	26 (56.5)	13 (28.3)	5 (10.9)	2 (4.3)	0	8.2	0	0	0

**Table 1** continued

Plots	Years	Cache sites	Total caches	Cache survival				Seedlings						
				≤10 days	11–20 days	21–30 days	>30 days	NS	MST (days)	Total	Survival (year)			
2008	2008	Total caches Vegetation type	61–100	103 (67.8)	59 (57.3)	13 (12.6)	7 (6.8)	20 (19.4)	4 (3.9)	9.8	1 (1.0)	1		
				152 (100.0)	88 (57.9)	26 (17.1)	12 (7.9)	22 (14.5)	4 (2.6)	9.2	1 (0.7)	1		
				43 (29.9)	27 (62.8)	8 (18.6)	2 (4.7)	4 (9.3)	2 (4.7)	8.5	0	0		
				5 (3.5)	2 (40.0)	1 (20.0)	2 (40.0)	0	0	10	0	0		
				84 (58.3)	56 (66.7)	12 (14.3)	8 (9.5)	3 (3.6)	5 (6.0)	8.1	2 (2.4)	1; 3		
				12 (8.3)	10 (83.3)	1 (8.3)	0	1 (8.3)	0	6.7	0	0		
				Substrate	Soil	69 (47.9)	51 (73.9)	13 (18.8)	0	3 (4.3)	2 (2.9)	7	1 (1.4)	3
					Litter	71 (49.3)	41 (57.7)	9 (12.7)	11 (15.5)	5 (7.0)	5 (7.0)	9.3	1 (1.4)	1
					Grass	4 (2.8)	3 (75.0)	0	1 (25.0)	0	0	7.5	0	0
					≤30	4 (2.8)	2 (50.0)	0	0	1 (25.0)	1 (25.0)	15	1 (25.0)	1
Shrubland	2007	Total caches Vegetation type	31–60	29 (20.1)	12 (41.4)	5 (17.2)	6 (20.7)	4 (13.8)	2 (6.9)	11.8	0	0		
				111 (77.1)	80 (72.1)	18 (16.2)	6 (5.4)	3 (2.7)	4 (3.6)	7.3	1 (0.9)	3		
				144 (100.0)	95 (66.0)	22 (15.3)	12 (8.3)	8 (5.6)	7 (4.9)	8.2	2 (1.4)	1; 3		
				60 (50.4)	29 (48.3)	10 (16.7)	8 (13.3)	11 (18.3)	2 (3.3)	10.8	0	0		
Grassland	2007	Substrate	Open	32 (26.9)	10 (31.3)	4 (12.5)	4 (12.5)	11 (34.4)	3 (9.4)	15	3 (9.4)	1; 2; >3		
				5 (4.2)	5 (100.0)	0	0	0	0	–	0	0		
				22 (18.5)	7 (31.8)	4 (18.2)	4 (18.2)	5 (22.7)	2 (9.1)	13.7	2 (9.1)	1; 1		
				56 (47.1)	27 (48.2)	5 (8.9)	2 (3.6)	18 (32.1)	4 (7.1)	13.3	3 (5.4)	1; 1; >3		
Shrubland	2008	Total caches Vegetation type	61–100	28 (23.5)	10 (35.7)	8 (28.6)	6 (21.4)	2 (7.1)	2 (7.1)	11.1	1 (3.6)	1		
				35 (29.4)	14 (40.0)	5 (14.3)	8 (22.9)	7 (20)	1 (2.9)	12.4	1 (2.9)	2		
				35 (29.4)	16 (45.7)	4 (11.4)	5 (14.3)	6 (17.1)	4 (11.4)	12.4	4 (11.4)	1; 1; 2		
				33 (27.7)	13 (39.4)	5 (15.2)	3 (9.1)	11 (33.3)	1 (3.0)	13.5	1 (3.0)	>3		
Grassland	2008	Substrate	Open	51 (42.9)	22 (43.1)	9 (17.6)	8 (15.7)	10 (19.6)	2 (3.9)	11.7	0	0		
				119 (100.0)	51 (42.9)	18 (15.1)	16 (13.4)	27 (22.7)	7 (5.9)	12.4	5 (4.2)	1; 1; 2; >3		
				119 (67.2)	80 (67.2)	27 (22.7)	9 (7.6)	2 (1.7)	1 (0.8)	7.3	1 (0.8)	1		
				31 (17.5)	11 (35.5)	5 (16.1)	4 (12.9)	6 (19.4)	5 (16.1)	13.8	5 (16.1)	1; 2; 3; >3		
Shrubland	2008	Substrate	Open grassland	2 (1.1)	1 (50.0)	1 (50.0)	0	0	0	7.5	0	0		
				25 (14.1)	7 (28.0)	10 (40.0)	5 (20.0)	3 (12.0)	0	11.1	0	0		
				74 (41.8)	36 (48.6)	20 (27.0)	10 (13.5)	7 (9.5)	1 (1.4)	9.3	1 (1.4)	1		
				74 (41.8)	36 (48.6)	20 (27.0)	10 (13.5)	7 (9.5)	1 (1.4)	9.3	1 (1.4)	1		

Table 1 continued

Plots	Years	Cache sites	Total caches	Cache survival				Seedlings			
				≤10 days	11–20 days	21–30 days	>30 days	NS	MST (days)	Total	Survival (year)
		Litter	73 (41.2)	48 (65.8)	16 (21.9)	5 (6.8)	2 (2.7)	2 (2.7)	7.6	2 (2.7)	3; >3
		Grass	30 (17.0)	15 (50.0)	7 (23.3)	3 (10.0)	2 (6.7)	3 (10.0)	9.7	3 (10)	1; 2; 2
		Canopy cover (%) ≤30	52 (29.4)	16 (30.8)	14 (26.9)	8 (15.4)	9 (17.3)	5 (9.6)	12.8	5 (9.6)	1; 2; 2; 3; >3
		31–60	28 (15.8)	20 (71.4)	5 (17.9)	3 (10.7)	0	0	7	0	0
		61–100	97 (54.8)	63 (64.9)	24 (24.7)	7 (7.2)	2 (2.1)	1 (1.0)	7.4	1 (1.0)	1
		Total caches	177 (100.0)	99 (55.9)	43 (24.3)	18 (10.2)	11 (6.2)	6 (3.4)	8.7	6 (3.4)	1; 1; 2; 2; 3; >3

All data presented as number (%). Canopy cover indicates the estimate of canopy coverage of high shrubs (≥1.5 m tall) and/or trees over the cache sites  
NS next spring, MST the median survival time using life-table test

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