

Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae)

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Abstract

Mast seeding is a very common phenomenon in plants that are dispersed by seed scatter-hoarding animals. This reproductive strategy has been explained as adaptation to satiate predators, and predator abundance affect the seed availability and the extent of satiation. We studied how mast seeding and rodent abundance co-influenced seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae) in the Dongling mountain of Beijing, China. We tracked the individual seeds marked with coded tin tags. The effects of seed crop size and rodent density were examined in May, August and October of a mast year (2000) and a non-mast year (2001). The seed removal rate was slower in mast seeding year than that in non-mast seeding year. There were more scatter hoarding and less larder hoarding with farther seed dispersal distance in the mast seeding year than that in the non-mast seeding year. The seed removal rates were positively correlated to the rodent abundance when data of six seasons of 2 years were pooled. There was high proportion of buried seeds in spring for both years. These results indicate that mast seeding and/or low rodent density increases scatter hoarding and dispersal distance, and then benefit seeding regeneration under effect of predator satiation; photoperiod seems not be very important in determining scatter hoarding activities of rodent in spring in the study region.

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1. Introduction

Tree seed predation and dispersal by mammals are key processes determining the variability in seed survival (Dirzo and Dominguez, 1986), and are considered to be major ecological forces in the structuring and maintenance of diversity in forest communities and the evolution of plants (Janzen, 1969, 1971; Howe and Smallwood, 1982; Fenner, 1985). Seed predation has the selective potential to shape phenological characteristics and to favor traits such as mast seeding that reduce seed predation (Curran and Leighton, 2000).

Mast seeding is a common phenomenon in plants that are dispersed by seed scatter-hoarding animals. It is the synchronous production of large seed crops, separated by years of greatly reduced seed production, by a population of plants. There have been several hypotheses offered to explain this

reproductive strategy in recent years. Predator satiation hypothesis proposes that mast seeding is an evolutionary response to intense seed predation. By storing resource during some years, mast-seeding species can produce massive crops in other years (Sork, 1993), which swamp local seed eaters with food and allow seeds to escape predation and successfully establish. Seed removal rates may decrease with increasing seed abundance (Crawley and Long, 1995; Theimer, 2001; Jansen et al., 2004). This hypothesis is one of the best established functional explanations for the mast seeding phenomenon (Kelly, 1994; Kelly and Sork, 2002). Mast seeding may enhance effective seed dispersal by scatter-hoarding animals (Jansen et al., 2004). However, most studies of mast seeding have focused on predator satiation (Sork, 1983, 1993; Crawley and Long, 1995), little is known how mast seeding and rodent abundance co-influence seed fates, and how they affect seed dispersal and caching behaviors by rodents (Theimer, 2001; Hoshizaki and Hulme, 2002; Vander Wall, 2002; Jansen et al., 2004).

In fact, rodent population fluctuation may also have an important impact on seed predation and seed dispersal

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(DeMattia et al., 2004). Brewer and Webb (2001) theorized that seed predation and scatter-hoarding of seeds could interact with rodent population dynamics in the recruitment of seedling. Rodent abundance may facilitate mast seeding effect because rodent high population is often 1 or 2 years delayed after mast seeding. For tree species with the mast seeding phenomenon, the plant population starves seed predators in non-mast years causing a decline in predator populations and satiated the decreased population of seed predators in mast years, resulting in a greater proportion of seeds surviving in mast years (Vander Wall, 2002).

Seasonality may be another important factor influencing seed predation and dispersal. Many food-hoarding animals, particularly those living at mid to high latitudes, disperse and store seeds on a seasonal cycle (Vander Wall, 1990). Photoperiod is thought to be an accurate indicator of food availability in seasons. Peak hoarding activity usually occurs during seasons with peak availability of seeds, and it may be induced by photoperiod through evolution. Then seasonal change in dispersal and hoarding may be more related to photoperiod (Vander Wall, 1990).

In 2000, there was a high seed crop of apricot (13.58 seeds/m²) and low rodent density (average trap success = 3.0%) in our study area nearby Beijing; while in 2001, there was a low seed crop of apricot (5.26 seeds/m²) and high rodent density (average trap success = 13.5%). Rodents only breed during May and August, and the rodent abundance is very low in spring, reaches peak in summer, and declines in autumn. Seed crop of apricot peaks in summer. We released tagged apricot seeds in field in May, August and October in 2000 and 2001. We aim to study: (1) how mast seeding affects the predation and dispersal of apricot seeds? We hypothesize that mast seeding slows seed removal, promotes scatter-hoarding and dispersal due to stimulation by abundant seeds; (2) how rodent abundance affect the predation and dispersal of apricot seeds? We hypothesize that high rodent abundance increases seed removal, decreases scatter-hoarding and dispersal because high rodent abundance reduce predator satiation effect of mast seeding. (3) How seasonality-related photoperiod affects the seed predation and dispersal of apricot seeds? We hypothesize that there will be no scatter hoarding in spring.

2. Methods

2.1. Study site and species

This study was conducted from May 2000 to June 2002 in Liyuanling of Dongling Mountains, about 120 km northwest of Beijing. The Liyuanling has an annual rainfall of 600 mm. Mean monthly minimum and maximum temperatures are -5.7 °C and 25.1 °C, respectively. Seed removal and dispersal were monitored in the vicinity of the Liyuanling (40°00' N, 115°30' E, ca. 1140 m elevation), in an area of sparse shrubland dominated by heterophyllous chastetree (*Vitex negundo*) and pubescent spiraea (*Spiraea pubescens*), with scattered lobeleaf elm (*Ulmus laciniata*), Liaodong oak (*Quercus liaotungensis*) and apricot (*P. armeniaca*) shrubs. The substrate in this

area is characterized by bare soil over limestone, scant herb layer on bare ground, and scattered boulders.

Apricot (*P. armeniaca*) is one of the common small trees or shrubs in mountainous areas near Beijing (Chen, 1997). Apricot can survive in harsh conditions with poor soil quality and low rainfall. Following a flowering season (from March to April), apricot fruit maturation and dropping begins in late June and continues through July. By mid summer, we rarely found edible apricot seeds on the ground. Apricot fruit contains a single seed (embryo plus endosperm) wrapped in a hard endocarp. We will use a general word "seed" to refer the whole propagule (embryo plus endosperm plus endocarp). After apricot fruit maturation, the pulp (mesocarp plus epicarp) will desiccate and dehisce, then the seeds will peel away from the pulp and become the smallest unit of dispersal. The apricot seeds germinate during May and June of next year. The seeds are ovoid and a bit flat. The thick and woody endocarp is smooth and hard, and its edge is sharp with grooves. The average weight of apricot seeds is 0.89 g (S.D. ±0.21, *n* = 50). The seed crops of apricot varied markedly year-to-year. In 2000, there was a high seed crop of apricot (13.58 seeds/m²) in our study area; while in 2001, there was a low seed crop of apricot (5.26 seeds/m²).

Primary dispersal of mature apricot seeds is by gravity. Then, seeds are consumed on the ground beneath fruiting trees of apricot by rodents like Korean field mouse (*Apodemus peninsulae*), Père David's rock squirrels (*Sciurotamias davidianus*), Chinese white-bellied rat (*Niviventer confucianus*), Siberian chipmunk (*Tamias sibiricus*), and probably by striped field mouse (*A. agrarius*), gray red-backed vole (*Clethrionomys rufocanus*), greater long-tailed hamster (*Tscheskia triton*) (Zhang and Wang, 2001a,b; Li and Zhang, 2003a,b). In this study area, only *A. peninsulae* was identified to be responsible for scatter-hoarding of apricot seeds, and the other rodent species are mainly seed eaters (Lu and Zhang, 2004, 2005). The endocarp of seed is so hard that only rodents are able to open it and birds were never observed to eat apricot seeds (Zhang and Wang, 2001a; Li and Zhang, 2003a).

2.2. Seed removal and fate experiments

In 2000, we established 20 seed stations with 15 m apart along a 300-m transect in the study area. In each seed station, 40 edible apricot seeds were deployed on the ground surface within 1 m² area in May, August and October, respectively. The experiment was repeated in 2001. All seeds were gathered >500 m away from the seed stations during early July 1999, 2000 and 2001. To identify the realistic results of seeds removal, we selected the transect where very few apricot seeds were produced and naturally dispersed for seed removal and fate experiments. The seeds were tagged by tin-tagging method modified after Zhang and Wang (2001a) and Zhang et al. (2005), so their fates could be tracked when they were removed. This method has been shown to have advantages over thread method (Xiao et al., 2006). Tiny holes were drilled on the edge of basal pericarp without destroying the inside kernel. And the seeds were tied through the holes with 3 cm × 1 cm pieces of

tin tags by using thin steel-wire of 3 cm long. Each tag had a unique code of metal-pen marks indicating deployment time and seed station number. The tag weights about 0.1 g. In the preliminary experiment, we placed the unmarked apricot seeds and metal-tagged seeds at the same time in each seed station in July 1999. After 16 days seed placement, the half-life time of unmarked seeds was 1.6 days, and that of metal tagged seeds was 2.1 days. It showed the metal-tagged seeds would be removed as readily as unmarked seeds. Thus the experimental treatment yields realistic results on the removal pattern of apricot seeds. The tin-tagged seeds are easy to find after being dispersed by rodents. If seeds are buried in the soil, the tin-tags are left on the surface of the ground.

After seed deployment, seed removal was checked along the transect about every 3 days during the first 20 days and about every 10 days during the following days. The census of seeds lasted for 2 months, but the census of seeds deployed in May of 2000 lasted for 3 months because the seed removal was slower. Seed fate, dispersal distance and cache microhabitat were recorded for each seed removed from seed station. The search areas were around the seed source stations to about 10 m beyond the most distant cache found in every direction. So missing seeds were likely taken into burrows.

Seeds remained in the station could have one of three fates. They could be: (1) remained intact on the surface of the floor (“surface”), (2) consumed on the spot and the fragments of seed hulls were left on the surface of the floor (“eaten”), (3) disappeared from seed stations (“removed”). We divided seeds removed from a station into the following four fates. They could be: (1) moved and left intactly on the surface of the floor (“surface”), (2) moved and the fragments of seed hulls were left with gnawing marks by rodents on the surface of the floor (“eaten”), (3) moved and scatter hoarded by shallow burial with tin-tag out of the ground surface (“buried”), (4) not relocated and taken underground into deep burrows (larder-hoarding) (“missing”). All seeds not buried were considered to be killed because when they were taken away stations, they were either consumed on the spot, were taken into deep burrows where they were eaten or do not survive as seedlings, or were assumed to be dead because intact seeds left by rodents on the ground surface desiccate and can not survive until next spring. We excavated the buried seeds and measured the depth of caches, and returned the seeds to the cache sites immediately. The cache sites were marked and rechecked if they would survive as seedlings next spring.

2.3. Trapping of small rodents

We monitored the rodent abundance for three different seasons (May, August and October) over 2 years (2000, 2001), by using wooden snare kill-traps baited with fresh, ripe apricot seeds. To minimize the effect of trapping on the rodent community in the plot where seeds were deployed, the trapping plot was established about 400 m away from the seed removal transect. The trapping plot was located in the same habitat as the seed removal experiments, so the rodent species composition and abundance in the trapping plot were similar

with those in the seed removal plot. In the trapping plot, four transects were selected and 25 traps with an interval of 5 m were set along each transect for two consecutive nights. The traps were checked every morning and the rodents captured were recorded.

2.4. Statistics

The data were analyzed using the SPSS10.0 statistical software. Log-rank and Breslow tests were used to compare the survival functions between three seasons, after the survival data had been stratified by seed station in order to remove station effects. The Log-rank test is more powerful in detecting difference in later survival, while the Breslow test is more powerful in detecting differences in early survival (Brewer, 2001). We determined the seed remaining days (SRD, one SRD = one intact seed remained in source seed station for 1 day). The Spearman’s test was used to analyse the correlation between SRD and rodent abundance. We used the proportion of rodent trapping success as a measure of rodent abundance.

Multinomial logistic regression was conducted on the effect of year and season on the number of scatter-hoarding seeds and larder-hoarding seeds. We employed the repeated measures analysis of variance (RMANOVA) to analysis the effects of year and season on the per-seed station mean distance of seeds removed. Fates of the seeds were treated as the repeated measure.

3. Results

3.1. Rodent population abundance

Rodent trapping yielded 99 small rodents including 59 *A. peninsulae*, 21 *N. confucianus*, 10 *T. triton*, 7 *A. agrarius* and 2 *Mus musculus*. In this study area, *A. peninsulae* was consistently the most abundant rodent (Fig. 1). Rodent trapping in three seasons over 2 years showed that there were significant interannual and seasonal variability in rodent abundance. The total trap success rate fluctuated from 3.0% in 2000 to 13.5% in 2001. More extensive trapping in this area has produced similar

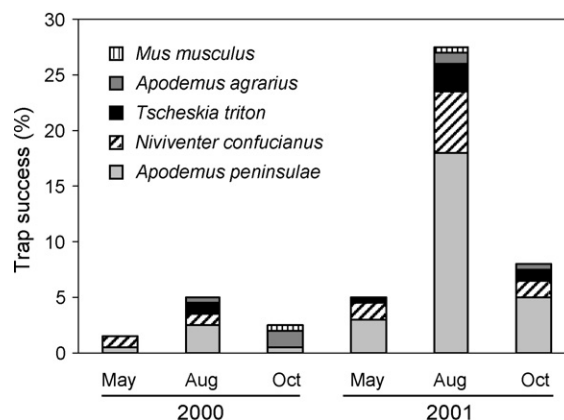


Fig. 1. Rodent community and abundance in May, August and October of 2000 and 2001.

rodent trap success during 1993–1995 (5.38%). These results indicate that the year of 2001 was a peak year for rodent population abundance. Although the rodent abundances are significantly higher in 2001 than in 2000, the trend was similar for 2 years with the rodent seasonal abundance decreasing in the following order: August > October > May. Because the seed crop of apricot was abundant and rodent population is low density in 2000, and vice versa in 2001, the predator satiation effect is much larger in 2000 than that in 2001.

3.2. Seed removal rate at seed stations

At the end of the experiment, nearly all of the labeled seeds had been removed from seed source stations. The percentage of seeds removed ultimately was similar between seed-rich year (98.42% in 2000) and seed-poor year (99.71% in 2001). Only very few seeds were remained (0–2.75%) or consumed (0–1.13%) on the spot (Table 1), indicating that the consumption by small rodents on seeds of *P. armeniaca* in seed source stations was very low. There was not significant difference in pre-removal seed consumption between seed-rich year and seed-poor year (one-way ANOVA: all $P < 0.05$ in May, August and October).

Seed crop size had an important effect on seed removal rate (the rate at which animal harvested seeds at seed station) (Fig. 2). Seeds deployed in seed-poor year of 2001 were removed significantly faster than seeds deployed in seed-rich year of 2000, for May (log-rank test: $\chi^2 = 1009.72$, $df = 1$, $P < 0.0001$; Breslow test: $\chi^2 = 776.87$, $df = 1$, $P < 0.0001$); for August ($\chi^2 = 1551.80$, $df = 1$, $P < 0.0001$; Breslow test: $\chi^2 = 1377.11$, $df = 1$, $P < 0.0001$); for October ($\chi^2 = 568.46$, $df = 1$, $P < 0.0001$; Breslow test: $\chi^2 = 634.82$, $df = 1$, $P < 0.0001$). These results indicate high-level predator satiation decreases seed removal rate, and vice versa.

As shown in Fig. 2, seeds deployed in August disappeared significantly faster than seeds deployed in October (log-rank test: $\chi^2 = 1466.70$, $df = 1$, $P < 0.0001$ in 2000, $\chi^2 = 395.98$, $df = 1$, $P < 0.0001$ in 2001; Breslow test: $\chi^2 = 1387.26$, $df = 1$,

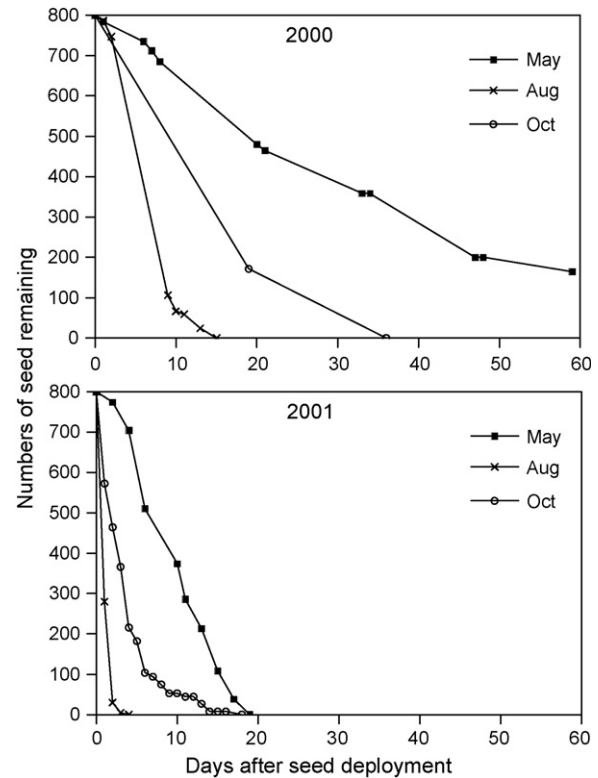


Fig. 2. Seed removal rates of apricot (*Prunus armeniaca*) in three seasons (May, August and October) during 60 days after seed placement in seed-rich year of 2000 and seed-poor year of 2001.

$P < 0.0001$ in 2000, $\chi^2 = 355.71$, $df = 1$, $P < 0.0001$ in 2001), and seeds deployed in October disappeared significantly faster than seeds deployed in May (log-rank test: $\chi^2 = 767.92$, $df = 1$, $P < 0.0001$ in 2000, $\chi^2 = 701.75$, $df = 1$, $P < 0.0001$ in 2001; Breslow test: $\chi^2 = 511.42$, $df = 1$, $P < 0.0001$ in 2000, $\chi^2 = 437.81$, $df = 1$, $P < 0.0001$ in 2001). The correlation between seed remaining days and rodent trap success was significant in 2001 ($r = -0.831$, $P < 0.00$, $n = 60$), and approximately significant in 2000 ($r = -0.229$, $P = 0.078$, $n = 60$).

Table 1
The seed fates of apricot (*P. armeniaca*) in seed stations at the end of experiments

Time of seed deployment	No. of seed deployment	Intact		Eaten		Removed	
		Number	Proportion (%)	Number	Proportion (%)	Number	Proportion (%)
2000							
May	800	22	2.75	7	0.88	771	96.38
August	800	0	0	9	1.13	791	98.88
October	800	0	0	0	0	800	100.00
Total	2400	22	0.92	16	0.66	2362	98.42
2001							
May	800	0	0	0	0	800	100.00
August	800	0	0	7	0.88	793	99.13
October	800	0	0	0	0	800	100.00
Total	2400	0	0	7	0.29	2393	99.71

Categories of seed fates: intact, eaten and removed.

Table 2
Multinomial logistic regression of buried and missing seeds in three seasons (May, August and October) over 2 years (2000 seed-rich year; 2001 seed-poor year) removed from seed stations ($n = 20$)

	df	Likelihood ratio tests χ^2	Buried		Missing		
			Wald	df	Wald	df	
Year	May	3	75.265***	10.075**	1	40.640***	1
	August	3	137.892***	18.697***	1	37.721***	1
	October	3	108.586***	37.049***	1	9.193**	1
Season	2000	6	309.830***	21.337***	1	180.764***	1
	2001	6	198.818***	0.330*	1	38.216***	1

All statistical significance level (P) are significant (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

These results indicate that rodent abundance significantly affects seasonal removal rates of seeds.

3.3. Post-removal seed predation and dispersal

The proportion of buried seeds (scatter-hoarding) and missing seeds (mostly larder-hoarding) of apricot differed significantly between years (Table 2, Fig. 3). In 2001, we found a total of 89 caches, whereas in 2000, the number of caches was up to 344 caches (3.9 times higher). The proportions of buried seeds in August and October were also significantly higher than that in 2001 (Fig. 3). The missing seeds were significantly more

in seed-poor year of 2001 (90.8%) than in seed-rich year of 2000 (65.5%) (Fig. 3, Table 2). These results indicate predation satiation increases scatter-hoarding. In years with mast seeding and low rodent density, there will be more scatter-hoarding, and vice versa.

The proportion of buried seeds (scatter-hoarding) and missing seeds (mostly larder-hoarding) of apricot also differed significantly among seasons (Table 2, Fig. 3). In seed-rich year of 2000, seeds deployed in August were buried significantly more than seeds deployed in October and May (multinomial logistic regression: Wald = 23.728, $P < 0.001$). In seed-poor year of 2001, seeds deployed in May were buried significantly more than seeds deployed in October and August (Wald = 1.966, $P < 0.05$).

3.4. Dispersal distances of seeds

All released seeds were found at distances from 1.0 m up to 35.0 m from the seed source stations. In 2000, the dispersal distance was 7.11 ± 3.41 m (mean \pm S.D.), while in 2001, it was 3.75 ± 2.32 m (mean \pm S.D.). The dispersal distance of buried, eaten and surface seeds differed significantly between 2000 and 2001 (all $P < 0.01$; Table 3, Fig. 4), indicating that predation satiation increases dispersal distance. The dispersal distance of buried, eaten and surface seeds differed significantly among seasons in 2001 ($P = 0.030$, Table 3, Fig. 4), not in 2000 ($P = 0.808$; Table 3, Fig. 4). The seeds deployed in October and August tended to be taken farther than seeds deployed in May when they were buried (one-way ANOVA: $P = 0.012$) in 2000.

3.5. Seed survival

All these buried seeds were scatter hoarded in shallow surface caches (1–3 cm deep). All caches contained only one seed each. There were only six seeds deployed in 2000 and 2001 germinated in next May (2000: $n = 2$ buried seeds deployed in August; $n = 1$ in October; 2001: $n = 3$ in May). All

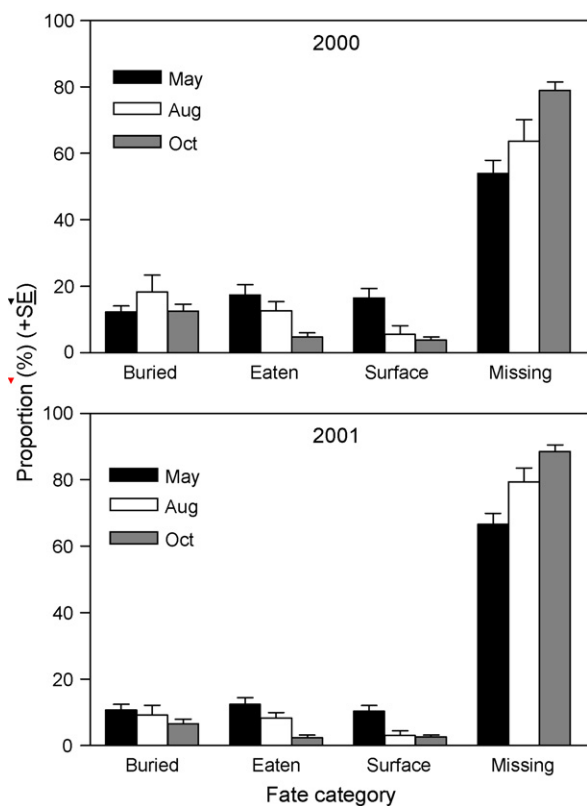


Fig. 3. Mean proportion (+S.E.) of *Prunus armeniaca* seeds that were removed from source stations, in four categories of seed fate: buried, eaten on the surface, intact on the surface and missing in May, August and October in 2000 and 2001.

Table 3
Repeated measures analysis of variance for the effect of year and season on the mean dispersal distance of *P. armeniaca* seeds, using fates (buried, eaten on the surface, intact on the surface and missing) as the repeated measure

Effect	Year	Source of variation	df	MS	F	P
Year	May	Year	1	130.688	11.162	0.002
		Fate	2	14.018	1.274	0.286
		Year \times fate	2	13.514	1.228	0.299
	August	Year	1	336.139	20.366	0.000
		Fate	2	51.095	2.583	0.082
		Year \times fate	2	28.681	1.450	0.241
	October	Year	1	569.678	37.186	0.000
		Fate	2	23.486	1.580	0.213
		Year \times fate	2	91.083	6.127	0.003
Season	2000	Season	2	3.076	0.214	0.808
		Fate	2	83.902	4.997	0.008
		Season \times fate	4	41.525	2.473	0.048
	2001	Season	2	54.642	3.729	0.030
		Fate	2	8.767	0.643	0.528
		Season \times fate	4	23.079	1.691	0.157

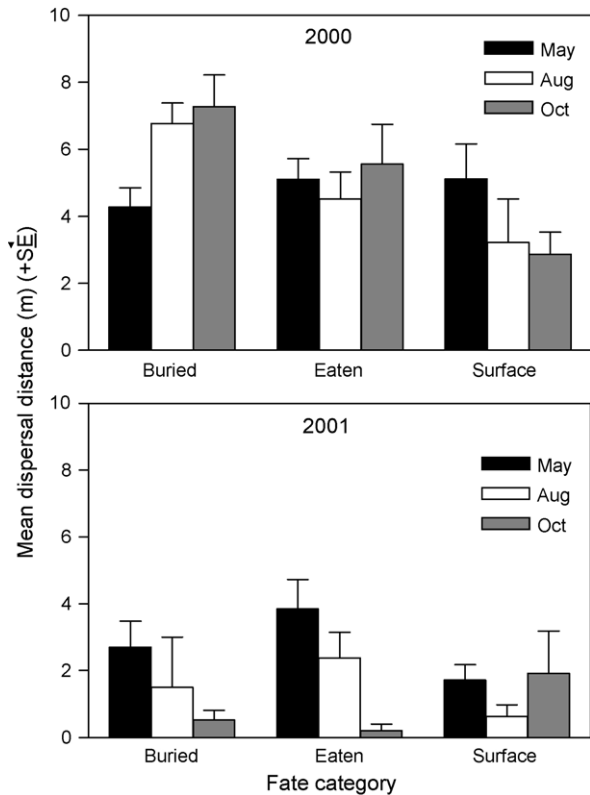


Fig. 4. Mean dispersal distance (+S.E.) of *Prunus armeniaca* seeds which were removed by small rodents in May, August and October in 2000 and 2001.

of the other seeds that had been buried were destroyed in surface or in burrows. All of seedlings emerged at the edge of the shrub canopy.

4. Discussion

In our study, seeds deployed in the mast seeding year (2000) were removed significantly slower than seeds deployed in the non-mast seeding year (2001). This observation conforms well to other previous studies (e.g. Crawley and Long, 1995; Jansen et al., 2004; Theimer, 2001). This also supports the prediction of the predator satiation hypothesis: a decrease in removal rates during mast years (Janzen, 1971; Kelly and Sork, 2002).

We found that mast seeding increased proportion of scatter hoarding and dispersal distance, which supports our hypothesis. Burial protects seeds from seed foraging and places seeds in a favorable environment for seed germination (e.g. Vander Wall, 1990). Greater scatter-hoarding increases the likelihood of seeds colonizing new sites (Stapanian and Smith, 1978). In mast year, there were more seed caches, and the rodents were unable to efficiently manage the numerous seeds, then some seeds have opportunities to establish seedlings (Jansen et al., 2004). Thus mast seeding benefits forest regeneration. Vander Wall (2002) also found dispersal distance was larger in mast seeding years, which supports the model of optimal caching density by Stapanian and Smith (1978).

The independent effects of rodent abundance on seed removal rate and dispersal distance in spring were well

illustrated in Figs. 2 and 4, since there was no seed rain in spring. High rodent density reduced dispersal distance though it increase seed removal rate. Rodent abundance may influence the mast seeding effect among seasons. For example, the proportion of buried seeds was the highest in August in 2000 with low rodent density, but the highest in spring in 2001 (Figs. 2 and 3), indicating that food availability or predation satiation affect survival of apricot seeds. The correlation between seed remaining days and rodent trap success was significant in non-mast year of 2001 ($r = -0.831$, $P < 0.001$), but not significant in mast year of 2000 ($r = -0.229$, $P = 0.078$).

Seed availability related photoperiod seemed not be important in determining scatter-hoarding of rodents in our study. We found very high proportion of buried seeds in spring for both years (Fig. 2). This result differs from other observations that peak hoarding activity of food-hoarding animals usually occurs during fall, coinciding with peak seed availability, and then decline to near zero in spring and summer (Vander Wall, 1990).

Very few tagged seeds became established by next spring, indicating the rodent predation is very high on apricot seeds. It is noticeable that all seedlings emerged at the edge of shrub cover. Several previous studies also found that seeds cached under shrubs have a higher chance of producing surviving seedlings than those cached in the open or under the canopy of trees (Callaway et al., 1996; Vander Wall, 2002). There was also a very serious drought happened during the spring 2001, which might be another reason for the very low seed survival even after mast seeding year. This results in no final difference of seed survival between mast seeding and non-mast seeding years.

In general, both mast seeding and rodent abundance have significant impacts on seed removal, seed hoarding and dispersal distances at yearly and seasonal levels. Photoperiod seems not very important in determining scatter hoarding activities of rodent in spring in the study region.

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