

Seed predation patterns favor the regeneration of dominant species in forest gaps compared with the understory in an oak-pine mixed forest

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Abstract Recent studies have demonstrated the higher likelihood of regeneration in forest gaps compared with the understory for the dominant species in pine-oak mixed forest. Here, we tested whether rodent seed predation or dispersal was beneficial for gap regeneration. We tracked the seed predation and dispersal of *Quercus aliena* var. *acuteserrata* and *Pinus armandii* using coded plastic tags in the forest understory close to gaps. Our results demonstrated that the proportions of initial buried seeds of both species were significantly more abundant in the forest understory compared with gaps. After seed caching, however, significantly lower proportions of the seeds of both species survived in the forest understory compared with gaps during the 30-day observation period. The final survival proportions of the seeds cached in the forest understory were lower than those cached in the gaps the next spring, which indicated that small rodents rarely retrieved scatter-hoarded seeds from forest gaps. Our findings suggest that rodent seed predation patterns contribute to the regeneration of the dominant species in gaps compared with

the understory in a pine-oak mixed forest. In the study area, reforestation usually involves planting seedlings but direct sowing in forest gaps may be an alternative means of accelerating forest recovery and successional processes.

Keywords Gap regeneration · *Pinus armandii* · Qinling Mountains · *Quercus aliena* var. *acuteserrata* · Seed dispersal

Introduction

Many plant species, such as trees with large seeds like acorns, depend on small rodents for seed dispersal in temperate ecosystems (Lida 1996; Sone et al. 2002; Gómez et al. 2003; Li and Zhang 2003; Lu and Zhang 2004; Xiao et al. 2005a; Abe et al. 2006; Liu et al. 2013) and tropical forests (Wenny 1999; Theimer 2001; Xiao et al. 2005b). Not all of the buried seeds are retrieved by small rodents and those that escape predation may establish seedlings in suitable conditions (Gómez et al. 2003; Li and Zhang 2003; Lu and Zhang 2004; Abe et al. 2006). From the plant's perspective, burial of seeds may be the most important benefit of rodent seed handling (Briggs et al. 2009). Thus, small rodents may play important roles during seed dispersal and subsequent plant regeneration (Price et al. 2000; Forget and Vander Wall 2001; Yi and Zhang 2008; Birkedal et al. 2009; van Ginkel et al. 2013; Yu et al. 2013a).

Howe and Smallwood (1982) suggested that the possible benefits of seed dispersal include: (1) escape from density-dependent mortality near the parent (escape hypothesis; Janzen 1970), (2) colonization of favorable sites during establishment (colonization hypothesis), and (3) directed dispersal to more favorable microhabitats (directed dispersal hypothesis). Seed dispersal to safe sites is one of the main advantages of seed dispersal because it may compensate for the significant loss to predation and other sources of mortality (Howe and Smallwood 1982; Wenny and Levy 1998; Lida 2006).

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However, low cache survivorship in previous studies has fueled the argument that scatter-hoarding rodents are believed to depredate most of the seeds they cache, and primary caches almost never persist until a seedling has established (Vander Wall and Jenkins 2003). It is not clear whether the survivorship of seed caches was affected by cache site (e.g., beneath the closed canopies or tree-fall gaps).

Canopy gaps are generally safe and favorable sites for seed establishment and survival (Hoshizaki et al. 1997; Lida 2006). Small rodents transport the seeds of various tree species into forest gaps increases the success of regeneration for gap-dependent tree species (Crawley 1992; Iida 2006). However, relatively open habitats (e.g., forest gaps) may have a higher predation risk for rodents because they are detected more easily by predators (Lima 1998; Bélisle and Desrochers 2002; Wilkinson et al. 2013). Ample evidence suggests that the predation risk may affect the seed-hoarding behavior of rodents (Li and Zhang 2003; Lu and Zhang 2004) and subsequent seedling recruitment (Duncan and Chapman 1999; Li and Zhang 2003). Thus, studies of the seed dispersal patterns in and around open woodlands are important for evaluating the role of seed dispersal by small rodents during the natural regeneration of woody plants (Scheper and Smit 2011; Smit and Verwijmeren 2011).

In China, *Quercus aliena* var. *acuteserrata* Maxim. and *Pinus armandii* Franch. are dominant species, and they contribute substantially to the stability and biodiversity of the forest ecosystem in the Qinling Mountains. These two species depend mainly on animals for the dispersal of their seeds (Chang et al. 2012a, b). Evidence suggests that the numbers of *Q. aliena* var. *acuteserrata* and *P. armandii* seedlings in forest gaps are greater than those found in the understory habitats, probably because of the better light and nutrient conditions in gaps (Xiao et al. 2002; Lan et al. 2006). The effects of gaps on seedling establishment have been investigated widely, but few studies have fully explored the ecological effects of *Q. aliena* var. *acuteserrata* and *P. armandii* seed dispersal by animals, and subsequent gap regeneration. Our knowledge of forest gap effects on the recruitment of trees and their relationship to seed dispersal patterns remains poor although forest gaps are common in the Qinling Mountains. In the present study, we used coded plastic tags to track seed predation and dispersal in the forest understory close to the gaps.

We compared differences in the seed consumption, removal, scatter hoarding, and survival of *Q. aliena* and *P. armandii* in different microhabitats to test whether buried seeds were more abundant in the understory and to determine their likelihood of survival in gaps in an oak-pine mixed forest. We hypothesized that animal seed predation patterns may benefit the regeneration of dominant species in forest gaps compared with the understory in an oak-pine mixed forest. We expect to obtain a better understanding of the real ecological effect of

habitat type on seed survival probability of *Q. aliena* var. *acuteserrata* and *P. armandii* in the Qinling Mountains.

Materials and methods

Study site

We conducted the experiment on the south facing slopes of the Qinling National Forest Ecosystem Research Station at Huoditang Forest (108° 21'–108° 39' E, 33°18'–33° 28' N), Ningshaan County, China. The elevation and slope gradient of the Huoditang Forest are 1,470–2,473 m and 15°–42°, respectively. The dominant soil is brown forest soil with an average thickness of about 50 cm. The principal soil-forming rocks include granite, gneiss, metamorphic sandstone, and schist. The annual average air temperature is 12.7 °C with extremes of maximum at 28.6 °C and minimum at –9.5 °C. Precipitation averages to 1,130 mm/year, mainly between July and September. Snowfall is common between late October and early April. The average annual humidity is 77 %. The forest was harvested during the 1960s and 1970s and much of the area is now covered by secondary growth. The dominant tree species are *Q. aliena* var. *acuteserrata*, *Pinus tabulaeformis* Carr., *P. armandii*, *Betula albosinensis* Burk., *Betula luminifera* H. winkl., *Picea wilsonii* Mast., *Abies fargesii* Franch., *Populus davidiana* Dode., *Toxicodendron vernicifluum* (Stokes) FA Barkley., and *Acer davidii* Franch. Forest cover and canopy closure are both >90 % (Yu et al. 2013b). Several rodent species coexisted in the study site; the dominant species are *Apodemus draco* Barrett-Hamilton., *Apodemus peninsulae* Thomas., *Sciurotamias davidianus* Milne-Edwards., and *Niviventer confucianus* Milne-Edwards. Previous study suggested that these rodents were likely to affect natural regeneration of the main tree species (Chang et al. 2012a, b; Yu et al. 2013a).

Seed marking

The mature and fresh seeds of *Q. aliena* var. *acuteserrata* were collected from the ground at our experimental sites during the seed rain period in 2012. The matured pinecones of *P. armandii* were bought from local farmers, and seeds were taken out for field release. We used water flotation and visual inspection to distinguish between sound and insect-damaged seeds. We randomly selected 1,000 sound *P. armandii* seeds (0.36±0.03 g) and *Q. aliena* var. *acuteserrata* acorns (1.70±0.04 g) and labeled them using slight modifications of the plastic-tagging methods reported by Zhang and Wang (2001) and Li and Zhang (2003). A tiny hole measuring 0.3 mm in diameter was drilled through the husk near the germinal disc of each seed, without damaging the cotyledon and the embryo. A flexible plastic tag (3.0×

1.0 cm, <0.1 g, 0.5-mm thickness) was tied through the hole in each seed using a thin 10-cm-long steel thread. To ensure that every seed could be easily relocated and identified, each seed was numbered consecutively and discriminatively with a tag. When rodents buried the seeds in the soil or litter, the tags are often still visible on the surface of the ground, which made them easy to find. Tagging has been shown to have a negligible effect on seed removal and hoarding behavior of rodents (Zhang and Wang 2001; Xiao et al. 2006).

Seed release and seed removal

The experimental site was an area of about 4.0 ha in the middle of the Qinling Mountains in China. Twenty seed stations were spaced 30–50 m apart along two transects established in the understory close to forest gaps (gap size = 100–150 m²) in an oak-pine mixed forest at the study site. The seed stations of transects are at similar distances (3–4 m) to gaps (Fig. 1). We placed 50 tagged seeds of each seed species (100 seeds total) at each seed station (1 × 1 m) and made them regularly spaced within stations. The total number of seeds released was 20(stations) × 50(seeds) × 2(species) = 2,000 seeds. Seed removal was checked daily until all of the seeds were removed or consumed. During each visit, we randomly searched the area around each seed station (radius within 40 m) with equal effort to retrieve removed seeds and record their fate. In each visit, we checked all seed stations as well as caches found in previous visits. The post-dispersal

seed fates were classified using nine categories: (1) intact in situ (IS), (2) eaten in situ (EIS), (3) cached in understory (CU), (4) cached in gaps (CG), (5) moved and eaten leaving only the plastic tags and seed fragments in understory (EU), (6) moved and eaten leaving only plastic tags and seed fragments in gaps (EG), (7) intact after removal to another location in the understory (IU), (8) intact after removal to another location in gaps (IG), and (9) missing where their true fates were unknown (M). When a cache was discovered, we carefully recorded the seed code numbers and measured the distance of the tagged seeds from their original seed stations and determined the cache location using a chopstick to mark the cache location, which was coded with the same number as the tag. The sticks were set 25 cm away from the seed caches. In the next visit, we also checked all the caches relocated in previous visits until the caches were removed or eaten by rodents. If a marked cache was removed, the area around the cache (radius within 40 m) was randomly searched. D5, D30, and NS represented the number of primary cached acorns that survived until day 5, day 30, and the next spring, i.e., March 2013. The survival rates of primary cached acorns on day 5, day 30, and the next spring were measured as the proportion of survived cached acorns relative to the total number of primary caches. Seed germination was surveyed during the following spring in 2013.

Identification of seed removers

To identify rodent species that might potentially remove the released seeds, 50 live steel wire traps (30 cm × 25 cm × 20 cm) baited with peanuts were placed along each of the two transects at an interval of 5 m apart on October 8–11, 2012 (just before the seeds' release). The traps were checked two times each day, i.e., at sunrise and sunset times. The captured animals were weighed and released immediately in situ. Trapping was conducted for 3 consecutive days. The total number of trapping days = 50 traps × 3 days = 150. This work was conducted based on Forestry Standards "Observation Methodology for Long-term Forest Ecosystem Research" of People's Republic of China (LY/T 1952-2011).

Data analysis

SPSS for Windows (Version 17.0) was used to perform the statistical analyses. The proportions of remaining, eaten, and cached seeds were arcsine-square-root transformed for statistical analysis. Cox Regression analysis was used to test for differences in the seed removal speeds between the two species. Generalized linear model (GLM)-univariate was used to test for differences in the proportions of the seed fates for each species and the seed dispersal distances of *Q. aliena* var. *acuteserrata* and *P. armandii*.

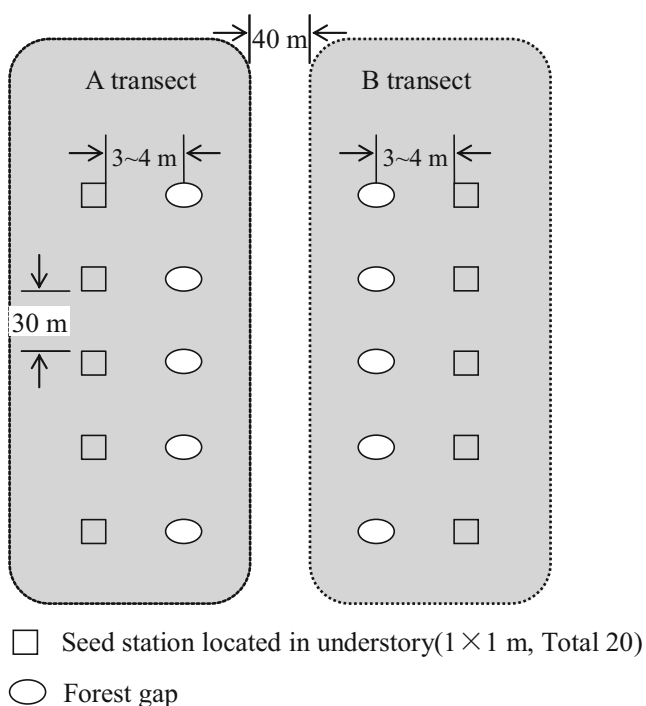


Fig. 1 Sketch map of the locations of seed stations in the experimental plots. Transects A and B mean two parallel transect lines

Results

Identification of seed removers

A total of 44 trappings of three rodent species were captured by live traps. Among them, *Apodemus peninsulae*, *Apodemus draco*, and *Sciurotamias davidianus* accounted for 65.9, 20.5, and 13.6 % of all captured animals, respectively.

Removal rates at seed stations

All of the released seeds were eaten or removed from the seed stations within 5 days after placement (Fig. 2). There was no significant difference in the removal speed at the stations for the two tree species ($Wald=0.866$, $df=1$, $P=0.352$).

Seed fates of *P. armandii*

The EIS proportion was affected significantly by the seed species ($F=4.195$, $df=1$, $P=0.047$) (Fig. 3). We retrieved 332 out of 550 *P. armandii* seeds (60.4 %) that were dispersed from the seed stations (450 *P. armandii* seeds were not dispersed but eaten in situ). The EU proportion for *P. armandii* seeds was significantly higher than EG when checked at 5 and 30 days (day 5: $F=13.846$, $df=1$, $P=0.001$; day 30: $F=7.604$, $df=1$, $P=0.009$) (Fig. 4). The CU proportion for *P. armandii* seeds was significantly higher than CG when checked at 5 days ($F=2.916$, $df=1$, $P=0.036$). However, the CU proportion for *P. armandii* seeds was significantly lower than CG when checked at 30 days and the next spring (day 30: $F=5.552$, $df=1$, $P=0.024$; NS: $F=4.750$, $df=1$, $P=0.036$). The IU proportion for *P. armandii* seeds was significantly higher than IG when checked at 5 days ($F=7.189$, $df=1$, $P=0.011$), whereas there were no significant differences when checked at 30 days and the next spring (day 30: $F=2.111$,

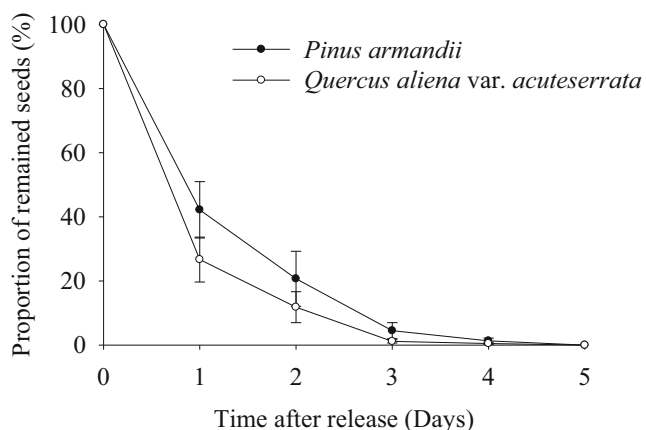


Fig. 2 Seed removal rates of *Q. aliena var. acuteserrata* and *P. armandii* after deposition at seed stations in the experimental plot. Data are expressed as mean±SE

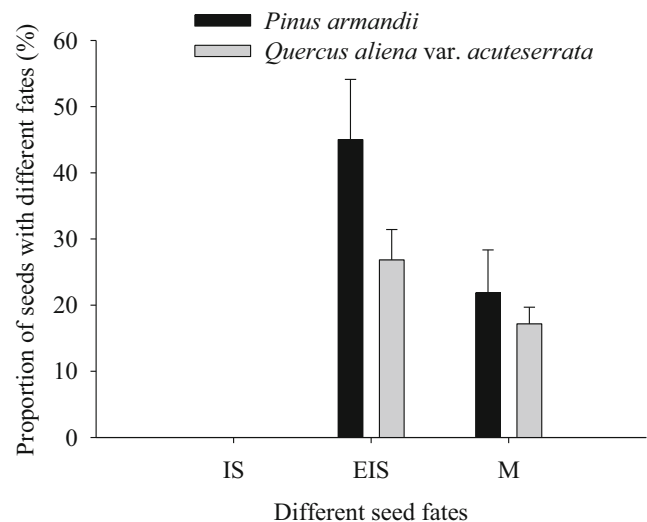


Fig. 3 Seed fates of eaten in situ and missing for *Q. aliena var. acuteserrata* seeds and *P. armandii* seeds by small rodents in the experimental plot. IS intact in situ, EIS eaten in situ, M missing. Data are expressed as mean±SE

$df=1$, $P=0.154$; NS: $F=0.731$, $df=1$, $P=0.398$) (Fig. 4). Of the 1,000 released seeds, no *P. armandii* seeds had survived to the seedling stage both in understory and gaps during the next spring.

Seed fates of *Q. aliena var. acuteserrata*

We retrieved 560 out of 732 *Q. aliena var. acuteserrata* seeds (76.5 %) that were dispersed from the seed stations (268 *Q. aliena var. acuteserrata* seeds were not dispersed but eaten in situ). The EU proportion for *Q. aliena var. acuteserrata* seeds was significantly higher than EG when checked at 5 and 30 days (day 5: $F=33.042$, $df=1$, $P<0.001$; day 30: $F=29.180$, $df=1$, $P<0.001$) (Fig. 4). The CU proportion for *Q. aliena var. acuteserrata* seeds was significantly higher than CG when checked at 5 days ($F=19.504$, $df=1$, $P<0.001$). However, the CU proportion for *Q. aliena var. acuteserrata* seeds was significantly lower than CG when checked at 30 days and the next spring (day 30: $F=6.574$, $df=1$, $P=0.014$; NS: $F=3.227$, $df=1$, $P=0.048$). The IU proportion for *Q. aliena var. acuteserrata* seeds was significantly higher than IG when checked at 5 days ($F=10.677$, $df=1$, $P=0.002$). Of the 1,000 released seeds, only three *Q. aliena var. acuteserrata* seeds had survived to the seedling stage and emerged in gaps during the next spring. Some seeds went missing, which may have emerged as seedlings outside the study area.

Seed dispersal distance

In total, 94.4 % of the removed seeds were dispersed within 20 m (Fig. 5). The maximum dispersal distances of *Q. aliena*

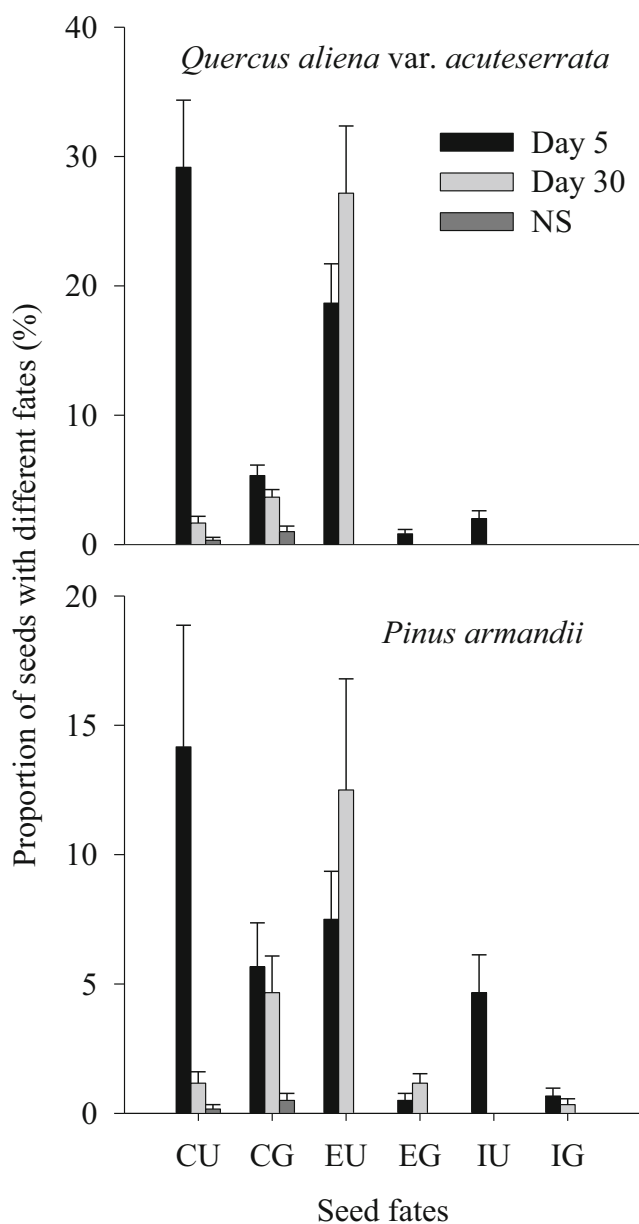


Fig. 4 Seed fates of *Q. aliena* var. *acuteserrata* seeds and *P. armandii* after dispersal by small rodents in the experimental plot. D5, D30, and NS represent the number of primary cached acorns that survived until day 5, day 30, and the next spring. Seed status include cached in understory (CU), cached in gaps (CG), eaten in understory (EU), eaten in gaps (EG), intact after removal to another location in the understory (IU), and intact after removal to another location in gaps (IG). Data are expressed as mean±SE

var. *acuteserrata* and *P. armandii* seeds reached 40.3 and 22.0 m, respectively. When checked at 5 days, the average dispersal distances were 8.18 ± 0.34 and 4.38 ± 0.25 m for the seeds of *Q. aliena* var. *acuteserrata* and *P. armandii*, respectively, which were significantly different ($F=66.314$, $df=1$, $P<0.001$). A total of 17 *Q. aliena* var. *acuteserrata* and 12 *P. armandii* seeds in primary caches were found to be recovered and subsequently recached in two micro-habitat types

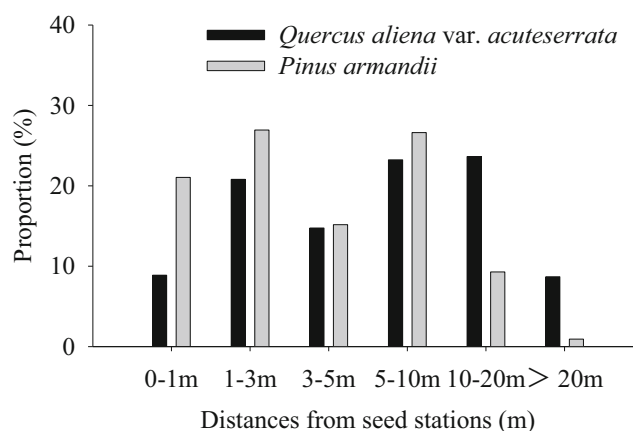


Fig. 5 Seed dispersal distances of *Q. aliena* var. *acuteserrata* seeds and *P. armandii* after primary dispersal from seed release stations in the experimental plot. Data are expressed as mean±SE

(i.e., CU, 16 *Q. aliena* var. *acuteserrata* seed secondary caches and 12 *P. armandii* seed secondary caches; CG, only 1 *Q. aliena* var. *acuteserrata* secondary cache) when checked at 30 days, which further extended the cache distributions. Mean dispersal distances of *Q. aliena* var. *acuteserrata* seeds increased from 7.6 m for primary caches to 11.3 m for secondary caches ($n=17$) and from 4.0 to 5.5 m for the seeds of *P. armandii* ($n=12$).

Discussion

Our study detected different dispersal patterns for *Q. aliena* var. *acuteserrata* and *P. armandii* seeds in the forest understory and gaps. The proportions of primary buried seeds of both species were significantly higher in the forest understory compared with forest gaps. After seed caching, however, the seeds of both species had significantly higher proportions of survival in gaps than in the forest understory during the 30-day observation period. In the next spring, the final survival rates of the seeds initially cached in gaps were higher than those cached in the forest understory, which indicated that small rodents rarely retrieved scatter-hoarded seeds from forest gaps. The higher activity (including seed predation) of small rodents below vegetation cover may be explained by the increased predation risk of rodents in relatively open habitats (Russell and Schupp 1998; Mohr et al. 2003; Lu and Zhang 2004). Our results suggest that predation risk of rodents may affect the seed-hoarding behavior (Li and Zhang 2003; Lu and Zhang 2004; Verdolin 2006) and the subsequent seedling recruitment (Duncan and Chapman 1999; Li and Zhang 2003).

Our results showed that the *Q. aliena* var. *acuteserrata* and *P. armandii* seeds were harvested rapidly from the seed stations at similar rates, which demonstrated the importance of

small rodents for the effective dispersal of the seeds of both tree species. Our observations agree with previous studies where fallen seeds were removed rapidly by rodents (Vander Wall 1990; Jansen and Forget 2001; Xiao et al. 2005b; Caccia et al. 2006; Chang et al. 2012a). Although we cannot fully exclude the possibility that other animals (e.g., wild pigs, cattle, Eurasian jays, and pheasants) than small rodents were responsible for the seeds removal of both tree species, we find this unlikely because their roles are probably negligible compared with small rodents in terms of their very few numbers in the study area (Chang et al. 2012a; Yu et al. 2013a). It is noticeable that the rodent density may have been overestimated because some animals might be recaptured.

We found that some of the released seeds of *Q. aliena* var. *acuteserrata* and *P. armandii* were transported into the gaps by small rodents. Our findings partly support previous studies, which showed that scatter-hoarding animals moved seeds from conspecific adult trees into different habitats, presumably to reduce pilfering. For example, fox squirrels moved *Juglans nigra* seeds from forests into adjacent prairies (Stapanian and Smith 1978), scatter-hoarding European jays moved *Quercus* seeds from oak woodlands into adjacent pine stands (Gómez 2003), and mice dispersed *Camellia japonica* seeds from old-growth forest into adjacent bamboo thickets (Abe et al. 2006) and *Quercus ilex* seeds away from the parent trees into open areas (Muñoz and Bonal 2011). We also found that the CU proportion was significantly lower than CG when checked at 30 days and the next spring, although initially higher in CU than in CG after 5 days. Previous studies have shown that not only dispersal but also removal of seeds is higher under dense vegetation such as shrubs (Iida 2006; Pérez-Ramos and Marañón 2008; Smit et al. 2006, Smit and Verwijmeren 2011), which is again mostly attributed to reduced predation risk (Manson and Stiles 1998). Our results indirectly have demonstrated that cache dynamics were lower in gaps than in the understory, which was beneficial to seeds of light-demanding species. Studies that address the importance of predation risks for functional connectivity often assume that the predation risk of rodents is high in certain landscape elements such as gaps (Bélisle and Desrochers 2002; Wilkinson et al. 2013). Tree-fall gaps may have higher predation risks for rodents and result in lower visitation frequency because they can be detected more easily by predators in these habitats (Lima 1998).

The EIS seed fates are probably explained by differences in the seed caching and pilfering behaviors of rodents with respect to large and small seeds. Previous quantitative studies have suggested that small seeds are more likely to be eaten in situ, whereas large acorns are more likely to be cached by rodents for future use (Vander Wall 1990; Jansen and Forget 2001; Xiao et al. 2005a; Caccia et al. 2006). Large seeds and nuts are probably more attractive food reserves for caching by rodents (Jansen and Forget 2001; Jansen et al. 2002, 2004).

Our study clearly showed that a very high proportion of the *P. armandii* seeds were eaten in situ, whereas more *Q. aliena* var. *acuteserrata* seeds were scatter-hoarded by rodents. Clearly, our results show that the roles of rodents during woody seed removal may vary according to the plant species, although they are dependent mainly on the seed size (Price and Jenkins 1986).

We found that *Q. aliena* var. *acuteserrata* seeds were dispersed for longer distances than *P. armandii* seeds, which supports the hypothesis of Jansen et al. (2002) that larger seeds are dispersed further from their parent trees (or seed stations). Seeds transported by small rodents had a lower survival rate in this study. Our observations agreed with previous studies, which showed that only 0.02–10 % of the removed seeds were able to establish seedlings (Hulme 2002; Jansen et al. 2002). The heavy drought during the spring of 2013 may have contributed to the low number of seedlings resulted from the three survived acorns. Some seeds may also have been cached at other locations outside the study area and emerged as seedlings there. Although these seedling proportions were not high, given the tens of thousands of seeds produced by each tree every year, the caching behaviors of rodents are likely to contribute significantly to seed survival and seedling establishment in natural conditions (Chang et al. 2012a, b). If the lower cache dynamics in forest gaps by small rodents is a general phenomenon, this dispersal pattern may compensate for the high mortality of seeds predated by small rodents.

In conclusion, our study found that more *Q. aliena* var. *acuteserrata* and *P. armandii* were buried in the understory during primary dispersal, but they had a lower survival rate than those buried in the forest gaps. Thus, these findings support the hypothesis that seed predation patterns may benefit the regeneration of dominant species in forest gaps compared with the understory in an oak-pine mixed forest. In the study area, reforestation usually involves planting seedlings, but direct sowing in forest gaps may be an alternative means of accelerating forest recovery and successional processes. Despite the effectiveness of animal seed dispersal on gap regeneration tested in the Qinling Mountains, future studies are needed to better understand the real ecological effect of habitat patches on the interaction with seed predators on seed cache dynamics and the subsequent seedling recruitment of animal-dispersed plants.

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