Dispersal and hoarding of sympatric forest seeds by rodents in a temperate forest from northern China

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Different species of forest trees exhibit great diversity in seed features, and diverse tactics of seed handling and dispersal are adopted by rodents. To better understand the discriminatory handling of sympatric seeds by rodents, seeds of four plant species, *Quercus variabilis*, *Prunus armeniaca*, *P. davidiana*, and *P. persica*, were released and tracked in a temperate forest in Yugong area of Jiyuan, Henan, north China. Results showed that: (1) seed removal rates of acorn (*Q. variabilis*), wild apricot (*P. armeniaca*) and wild peach (*P. davidiana*) differed significantly, while almost all (99%) peach seeds (*P. persica*) remained *in situ*; (2) acorns (55%) were eaten more than wild apricot (4%) and wild peach (0%), whereas seeds of wild apricot (62%) were scattered-hoarded more than wild peach (13%) and acorns (36%); hull thickness exerted a nonlinear influence on eating and scatter-hoarding; (3) rodents transported wild peach seeds farther (3.81 m ± 2.44 SE) than wild apricot seeds (3.41 m ± 2.05) and acorns (2.49 m ± 2.37); (4) rodents buried multiple wild apricot seeds in some caches, but seeds of wild peach and acorn were stored singly. Results indicated that, for sympatric seeds, rodents would adopt discriminatory processing and storing strategies in eating, burying, dispersal and cache size. Seeds with medium hull thickness were more likely to be dispersed and to survive, and consequently have higher probability of future germination and seedling establishment.

Keywords: Seed Traits, Rodent, Discriminatory Dispersal, Cache Size, Dispersal Distance, Seed Fate

Introduction

Interactions between forest seeds and rodents have been widely reported (Vander Wall 1990, Boman & Casper 1995, Moles et al. 2003, Cao et al. 2011, Carlo et al. 2011, Heleno et al. 2011, Puan et al. 2011, Yi et al. 2012). Many granivorous rodents are known to store large amounts of plant seeds in the field during seed-rich period (Vander Wall 1990, Longland & Clements 1995, Li & Zhang 2003, Zhang et al. 2008, Gutiérrez-Granados 2011, Meng et al. 2012). Rodents' scattering-hoarding behavior often plays a crucial role on seed dispersal and plant recruitment because scatter-hoarded seeds are buried in microhabitat with temperature and moisture favorable to seed survival and germination (Reichman 1979, In-ouye et al. 1980, Price & Jenkins 1986, Schupp & Fuentes 1995, Chambers 2010, Jansen & Forget 2001, Hollander & Vander Wall 2004, Xiao et al. 2006). However, in the field, morphological and physiological differences commonly occur among seeds of sympatric tree species (Vander Wall 2001, Zhang & Zhang 2008). Thus, seed-eating rodents usually balance between benefits, *e.g.* net energy income and nutrients, and costs, *e.g.* predation risks, during seed scattering-hoarding (Lima & Dill 1990, Jacobs 1992, Hadj-Chikh et al. 1996, Sivy et al. 2011). Seed traits can influence animals' decision concerning seed selection, eating or hoarding (Jacobs 1992, Hadj-Chikh et al. 1996, Smallwood et al. 2001). On one hand, seeds with thinner hulls and lower handling costs are disadvantageous for long-term storage and are more likely to be consumed immediately (Zhang & Zhang 2008, Chen & Chen 2011, Rusch et al. 2013). On the other hand, seeds with thick hulls are often lardered or scattered-hoarded because of long-term storage advantage (Steele et al. 1996, Sun & Chen 2000, Lu & Zhang 2005, Zhang & Zhang 2008). Seeds with too thick husks are, however, disadvantageous for long-distance dispersal and feeding by rodents because of lower rewards and high predation risks (Zhang & Zhang 2008, Rusch et al. 2013).

Sympatric animal and plant species have adaptively co-evolved traits to decrease excessive ecological overlap and avoid intra- and inter-specific competitions (Smith & Reichman 1984, Vander Wall 2001). In the forest, plants disclose seed features to attract possible dispersers but avoiding over-predation at the same time; correspondingly, rodents discriminate seeds depending on their palatability, nutrition and physical characteristics (Vander Wall 1990, Muñoz et al. 2012, Rusch et al. 2013). For instance, small rodents feed mainly on small-sized seeds, while larger rodents consume seeds of various sizes (Vieira et al. 2003).

Studies carried out so far on seed selection and dispersal of sympatric seeds by rodents are limited (Chen & Chen 2011, González-Rodríguez & Villar 2012, Yang et al. 2012, Rusch et al. 2013) and far from fully depicting the wide variation in the hoarding behavior of rodents in different geographical areas. Hull thickness has been reported to significantly affect seed dispersal (Zhang & Zhang 2008), while other investigations have obtained conflicting result (Yang et al. 2012). To further understand discriminatory hoarding strategies of rodents, seeds from four sympatric forest species differing in seed hull thickness were released and tracked in a temperate forest of China. We expected that rodents were preferably eating on seeds with thinner hull and hoarding medium-thick hull seeds, while seeds characterized by over-thick hull were unlikely to be selected by rodents.

Materials and methods

Study site

The study was conducted in the area of Yugong (750 m a.s.l., 112°16' E, 35°12' N) in Jiyuan, Henan province, China. This area is dominated by northern temperate zonal continental monsoon climate. The annual average temperature is 14.3 °C, and average annual precipitation about 600-700 mm. Vegetation can be classified into three types: coniferous forests, broad-leaved forests and shrubs. Our study site fell in a secondary broad-leafed deciduous forest, where the

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Tab. 1 - Seed characteristics of the four investigated species.

Species	Seed weight (g)	Kernel weight (g)	Thickness of seed hull (mm)
Prunus persica	3.84 ± 0.11	0.37 ± 0.01	4.95 ± 0.06
Prunus davidiana	2.32 ± 0.07	0.35 ± 0.01	3.72 ± 0.07
Prunus armeniaca	1.03 ± 0.04	0.33 ± 0.01	1.48 ± 0.03
Quercus variabilis	3.11 ± 0.17	2.76 ± 0.31	0.84 ± 0.04

most common tree species included *Prunus davidiana, P. armeniaca, Quercus variabilis, P. persica, Populus tomentosa, Robinia pseudoacacia* and *Platycladus orientalis*; while brushwood included mainly *Lespedeza bicolor, Cotinus coggygria, Ziziphus jujuba* var. *spinosa* and *Rosa xanthine* (Zhao et al. 2009, Ma et al. 2010). The field experiment was carried out in a plot (about 200 x 300 m) where *Q. variabilis* was the dominant tree species; other species like *R. pseudoacacia, P. persica, Vitex negundo* var. *heterophylla, R. xanthina* and *C. coggygria* were sparsely distributed in the plot. Two parallel transects (separated by at least 25 m) were established, and 5 seed stations (1 x 1 m) were selected along each transect (separated by at least 25 m).

Seed collection and preparation

Ripe seeds of wild apricot (*P. armeniaca*), wild peach (*P. davidiana*), peach (*P. persica*) and Cork oak (*Q. variabilis*) were collected from different trees during the fruiting season, and kept at field temperature to prevent deterioration and germination.

Healthy seeds of the four species were selected randomly for field tests. All selected seeds were tagged with white plastic tags as described in Zhang & Wang (2001) and Xiao et al. (2006). A hole of 0.3 mm in diameter was drilled through the husk far from the embryo of each seed, without damaging the cotyledon and embryo. A plastic tag (2.5 x 3.5 cm, < 0.3 g) was tied through the hole of each seed using a thin 10cm-long steel thread. The plastic tag was consecutively numbered to allow all seeds to be easily relocated and identified.

Seed releasing and tracking

In September 2011, in each seed station twenty seeds per species were released together on the ground surface, for a total of 80 seeds per station. Seeds were checked every five days for two months, and their fates were recorded. Status of the released seeds was defined as: (i) eaten (E) - seeds with kernel eaten at or close to the seed station; (ii) scatter-hoarding (SH) - seeds still intact but buried in soil; (iii) abandoned on the surface (AS) - seeds abandoned on the ground surface after removal; (iv) remained *in situ* (R) - seeds not removed from the station; and (v) missing (M) - seeds removed but not found (Lu & Zhang 2005, Yi & Zhang 2008).

Rodent trapping

Main rodent species recorded in the study area are *Apodemus peninsulae, A. agrarius, Niviventer confucianus, Sciurotamias davidianus, Cricetulus triton* and *Eutamias sibiricus* (Zhao et al. 2009, Ma et al. 2010). The potential rodent species and their relative abundance occurring during the experiment were monitored with 80 live traps (30 x 13 x 12 cm) baited with peanut (*Arachis hypogaea*): 20 traps (separated by at least 5 m) set up in each of four transects (separated by at least 25 m). The traps were examined twice a day (dawn and dusk), and rodent species and gender recorded. Trapped rodents were marked and released *in situ*.

Trapping was conducted for three consecutive days at the end of the experiment to reduce possible interferences with field observations.

Seed traits

Seed weight, kernel weight and husk thickness were measured in 100 healthy seeds per species randomly chosen. Seed and kernel weight was measured by an electronic scale (± 0.01 g), whereas husk thickness was measured with an electronic vernier caliper (± 0.01 mm).

Data analyses

Statistical analyses were carried out by SPSS for Windows (Version 16.0). Kaplan-Meier was used to analyze seed removal curves of different species. General linear model - multivariate test (MANOVA) was used to test possible differences of seed fate among species. One-way ANOVA was used to test differences among different species in dispersal distance and cache size (*i.e.,* number of seeds in one scatter-hoarded cache site - Vander Wall 1990). LSD *post-hoc* test was used for pairwise comparison of means in MANOVA and ANOVA. The occurrence of possible relations between hull thickness and scatter-hoarding or eating was analyzed by using a nonlinear regression analysis.

Results

Trapped rodents and seed traits

Two species of rodents, *A. peninsulae* and *S. davidianus*, were trapped at the study area, with a total trap success rate of 1.3% and 4.2%, respectively.

Seeds of the four tested plant species differed greatly in morphological traits (Tab. 1), in terms of, *e.g.,* seed weights (peach > acorn > wild peach > wild apricot) and hull thickness (acorn < wild apricot < wild peach < peach).

Removal dynamics of tested seeds

Most of acorns (96%) and wild apricots (89%) were removed within 25 days, while 99% of released peach seeds remained *in situ*. Removal rates of the released seeds differed significantly among tree species (cork oak, wild apricot and wild peach: $\chi^2 = 107.036$, df = 2, $P < 0.001$ - Fig. 1). The mean survival time of acorns (8.60 ± 0.39 days) was significantly lower than wild apricots (20.90 ± 0.53 days; $\chi^2 = 124.062$, df = 1, $P < 0.001$) and wild peaches (24.50 ± 1.69 days; $\chi^2 = 33.703$, df = 1, $P < 0.001$ - Fig. 1).

Fate of released seeds

Rodents showed a preference for wild apricot and cork oak higher than wild peach ($F = 45.559$, df = 2, $P < 0.001$ - Fig. 2). The proportion of R was significantly higher in
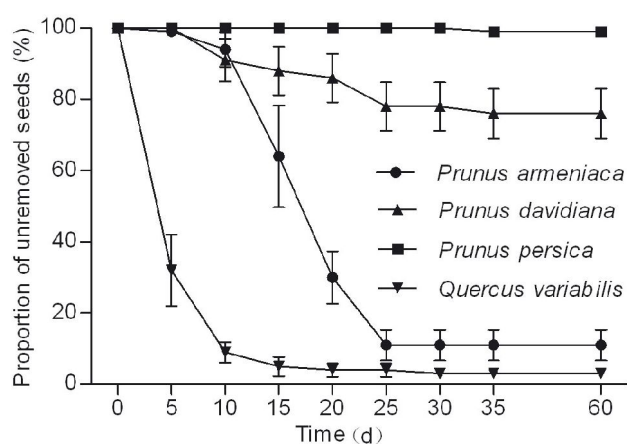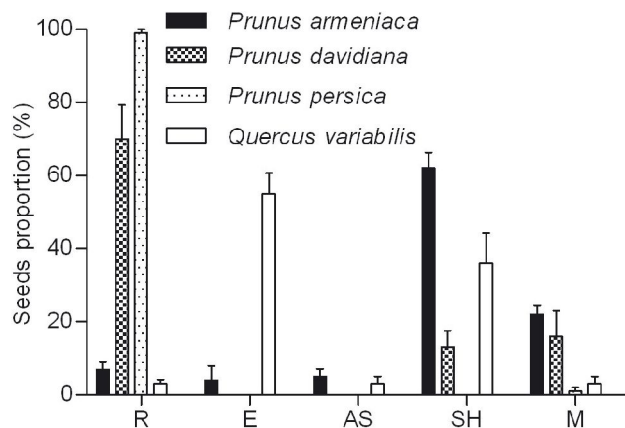

Fig. 1 - Removal dynamics of different seed species.

Fig. 2 - Fate of released seeds after removal by rodents. (R): remained *in situ*; (E): eaten; (AS): abandoned on the surface; (SH): scatter-hoarding; (M): Missing.

wild peach (70%) than in wild apricot (7% - $P < 0.001$) and cork oak (3% - $P < 0.001$ - Fig. 2).

The proportion of E was significantly different among seed species (cork oak, wild apricot and wild peach - $F = 58.165$, df = 2, $P < 0.001$), with cork oak (55 %) higher than wild apricot (4 % - $P < 0.001$) and wild peach (0 % - $P < 0.001$ - Fig. 2). Moreover, the proportion of E was strongly correlated ($R^2 = 0.8265$) with hull thickness ($y = -40.678 \cdot ln\, x + 47.069$).

Except for peach seeds, many seeds of wild apricot, wild peach and cork oak were in status of SH, with significant differences among tree species ($F = 16.541$, df = 2, $P < 0.001$). The proportion of SH cork oak (36 %) and wild apricot (22 %) were much higher than wild peach (13 % - $P < 0.001$ - Fig. 2). Also in this case the proportion of SH seeds was correlated ($R^2 = 0.7236$) with the hull thickness ($y = -9.75 \cdot x^2 + 33.05 \cdot x + 18.25$).

Variation in cache size among tested seeds

Most scattered cache sites (89.29 %) of wild apricot contained only one seed, whereas 10.71 % contained two or three seeds; cache sites of both wild peach and cork oak had only one seed (Tab. 2). Significant differences were found among the three species for two-seed caches ($F = 3.750$, df = 2, $P < 0.05$ - Tab. 2).

Dispersal distances of tested seeds

The highest dispersal distance of the removed seeds was less than 15 m, although more of 95 % of seeds were dispersed less than 9 m. The mean dispersal distance was 3.41 ± 2.05 m (wild apricot - n = 58), 3.81 ± 2.44 m (wild peach - n = 14) and 2.49 ± 2.37 m (cork oak - n = 57) respectively, with significant differences among species ($F = 3.365$, df = 2, $P < 0.05$). Especially, the mean dispersal distance of cork oak was remarkably lower than that of the other species ($P < 0.05$ - Tab. 2).

Discussion

Under natural conditions, different plant seeds usually coexist in given geographical area and provide potential food resources for granivorous animals (Smith & Reichman 1984, Lima & Valone 1986, Vander Wall 1990, Shimada 2001). However, sympatric seeds may differ notably in palatability and nutrition value (Vander Wall 1990). To survive and reproduce, seed-eating animals had developed numerous adaptations in treating and consuming various sympatric seeds (Chen & Chen 2011, González-Rodríguez & Villar 2012, Yang et al. 2012).

Discriminatory handling on sympatric seeds

Our results revealed that rodents displayed discriminatory processing strategies in eating and hoarding sympatric forest seeds. Rodents preferred to consume acorns having thinner hulls, while scatter-hoarded wild apricot and wild peach seeds having thicker hulls, and ignored peach seeds with the thickest hulls. The results supported our predictions and indicated that thickness of seed hull produces a nonlinear effect on the scat-

ter-hoarding behavior of rodents. This selectivity in seeds consumption and dispersal may be explained by the trade-off between costs and benefits in handling seeds. Because acorns are vulnerable to microorganism infection and deteriorate easily, they are not suitable for long-term storage (Steele et al. 1996, Sun & Chen 2000, Lu & Zhang 2005, Zhang & Zhang 2008). Their weak hulls are especially convenient for instant consumption by predators. Furthermore, seeds of wild apricot and wild peach are covered with medium-thickness hulls, determining higher consumption costs, as well as longer edibility-guarantee-period (Jacobs 1992, Hadj-Chikh et al. 1996, Lu & Zhang 2005, Abe et al. 2006). Almost all peach seeds with very thick hulls were rejected by rodents. This could possibly be attributed to: (1) lower reward and higher predation risk (Lima & Valone 1986, Zhang & Zhang 2008); (2) the influence of alternative food resources within habitat during study period; or (3) the unsuitable tooth structure of these rodent species to consume such seeds, on which further investigation is needed.

Difference in cache size

In this study, all seeds of cork oak and wild peach were buried singly in each cache site, whereas multiple seeds of wild apricot were found in scatter-hoarded caches. The size of apricot seeds was greatly smaller than that of cork oak and wild peach, so seed size may have accounted for the differentiation in cache size. It is difficult for small rodents to carry many big-sized seeds at one time and the number of seeds in one cache site decreases with increasing seed size (Vander Wall 1990, Mack 1998, Vander Wall 2003).

Differentiation in hoarding strategy to sympatric species seeds might affect seed fate (Xiao et al. 2004, 2005, Muñoz et al. 2012, Rusch et al. 2013). Single-seed caches are favorable for seed germination and seedling establishment compared to multiple-seed and larger-hoarded caches (Hollander & Vander Wall 2004). Seedlings emerging from clumped seeds often suffered a high mortality rate because of intense competition for limited resources and space (Howe 1989). Also, larger caches were more likely to be found and plundered by conspecific and interspecific foragers (Vander Wall 1993a).

Variation in dispersal distance

Dispersal enhances the spreading of plant seeds far away from the mother trees and therefore boost the species colonization (Nilsson 1985, Vander Wall 1993b). Some studies demonstrated that larger seeds are transported at a greater distance than smaller ones (Xiao et al. 2005); nevertheless other studies showed that seeds with higher predation reward were usually transported and stored at farther distance (Lima & Dill 1990,

Tab. 2 - Scatter-hoarded cache size of seeds from different tree species. (*): significant differences among species (P<0.05).

Species	Dispersal (m)	Cache size (%)			
		1 seed	2 seeds	3 seeds	>3 seeds
Prunus armeniaca	3.41 ± 2.05	89.29	8.93*	1.78	0
Prunus davidiana	3.81 ± 2.44	100	0	0	0
Quercus variabilis	2.49 ± 2.37*	100	0	0	0

Hadj-Chikh et al. 1996, Yang et al. 2012). However, we founded that wild peach and wild apricot seeds were moved and hoarded farther than acorns. The reasons might be that seeds of wild peach and wild apricot had moderately thick hulls and were suitable for long-term hoarding compared to acorns. So, dispersal distance may be affected by joint factors such as seed size (Xiao et al. 2005), costs and rewards of hoarding (Jacobs 1992, Hadj-Chikh et al. 1996, Sivy et al. 2011, Yang et al. 2012), and the suitability of seeds to storage (Lu & Zhang 2005).

Conclusions

Rodents exhibited discriminatory selection to sympatric plants when consuming and hoarding their seeds. Consequently, the influence of rodents on seed fate would vary according with seed traits. For instance, hull thickness would produce a non-linear effect on seed dispersal, with species having medium thickness hull being advantaged in seed dispersal and survival. This research might be useful in explaining the co-evolution of plants and animals, and broaden our understanding to the co-existence mechanisms of sympatric forest trees with heavy seeds.

Acknowledgments

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