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ORIGINAL PAPER

Repeated radicle pruning of *Quercus mongolica* acorns as a cache management tactic of Siberian chipmunks

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Abstract Many rodents hoard seeds as a means of ensuring food availability during scarcity. Siberian chipmunks (*Tamias sibiricus*) feed on acorns of white oak *Quercus mongolica* and hoard them for future use. Such caches may deteriorate due to the early germination of the acorns in autumn, which can be inhibited by radicle pruning or embryo excision. Siberian chipmunks are found to frequently prune the radicles of germinated acorns of *Q. mongolica*; however, whether this behavior is a kind of cache management tactic remains unclear. Here, we performed semi-natural enclosure and field experiments to test the role of radicle pruning in cache management of *T. sibiricus*. We found that *T. sibiricus* preferred non-germinated acorns and tended to prune radicles of germinating acorns when scatter-hoarding them, but did not perform the behavior of embryo excision by squirrels. Both semi-natural enclosure and field experiments showed that *T. sibiricus* not only pruned radicles repeatedly but removed radicles varied in length from acorns, which significantly postponed acorn germination and radicle growth. These observations suggest that radicle pruning would be an evolutionary tactic for cache management of Siberian chipmunks.

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Introduction

Small mammals play a dual role both as seed dispersers and seed predators in the mutual interaction with plant species bearing large-sized seeds (McEuen and Steele 2005). Many small rodents and bird species mitigate seasons of food shortage by hoarding seeds in their caches or larders to use as long-term food supplies (Jansen et al. 2006; Moore and Swihart 2006). However, germination of seeds in caches can be a major cause of food loss to hoarding animals (Elliott 1978; Fox 1982; Hadj-Chikh et al. 1996). Therefore, storage life will become an important factor for hoarding animals when selecting seeds for food storage (Reichman 1988; Gendron and Reichman 1995; Hadj-Chikh et al. 1996; Chang et al. 2009). Acorns of many white oak species germinate in autumn soon after they fall (Fox 1982; Hadj-Chikh et al. 1996; Steele et al. 2001a, b; Xiao et al. 2009), resulting in food loss because nutritional reserves in acorn cotyledons are quickly transported into an inedible robust taproot (Fox 1982; Steele et al. 2001a; Jansen et al. 2006; Xiao et al. 2009). Previous studies in the New World (Elliott 1978; Fox 1982; McEuen and Steele 2005; Steele et al. 2001a, 2007) have shown that various rodent species in different systems can slow or stop germination of cached seeds of particular fast-germinating tree species by pruning the radicle or sprout, or even by removing the entire embryo (Vander Wall 1990; Jansen et al. 2006; Xiao et al. 2009). Naïve tree squirrels are found to attempt embryo excision (Steele et al. 2006), supporting a hypothesis that squirrels show specific behavioral adaptations to quick germination of acorns of white oak species.

Siberian chipmunks (*Tamias sibiricus*), feeding on acorns of Mongolian oak (*Quercus mongolica*), scatter-hoard seeds in autumn and hibernate in a permanent burrow with a food supply in winter (Jin et al. 2004). Mongolian oak acorns do not undergo autumn dormancy and cached acorns germinate quickly, reducing the value of this stored food supply. Due to the fact that many rodents are sensitive to germination schedules (Fox 1982; Jansen et al. 2006), intervention in germination by Siberian chipmunks might be expected if seed modification slows or stops germination of cached acorns of *Q. mongolica*. However, no literature currently reports the behavior of embryo excision by chipmunks to cope with rapid germination of seeds in caches. Natural history observations on Siberian chipmunks both in the field and enclosures in the past 3 years indicate that the behavior of radicle pruning is frequently found in this species (personal observation). However, whether the behavior of radicle pruning represents the same evolutionary cache management tactic as embryo excision by squirrels remains unclear. Herein, we sought to investigate whether and how radicle-pruning behavior functions as a cache management tactic by Siberian chipmunks. We attempted to test the following four alternative hypotheses to potentially explain this behavior: (1) Siberian chipmunks prefer non-germinated acorns over germinating ones for caching because they require no or less investment in surveillance and interventions when caching; (2) due to the high regeneration capacity of pruned acorns, chipmunks are expected to repeatedly prune the radicles; (3) repeated radicle pruning and removal of long radicles can slow down or stop germination of acorns; and (4) radicle pruning would be an evolutionary tactic of Siberian chipmunks to manage their scatter caches.

Materials and methods

Study site

The study was conducted in September 2009 in the Dongfanghong Forestry Center (mean elevation of 750 m, 45°58′N, 129°08′E) in the Dailing District, Yichun City, Heilongjiang Province, northeast China. The climate at the site is dominated by the north temperate zonal monsoons with long, severe winters and short cool summers. The annual average air temperature is 1.4°C with a maximum of 37°C and minimum of −40°C. Annual precipitation averages 650 mm, 80% of which falls between May and September. The zonal vegetation is characterized by secondary broad-leaf and mixed conifer forests. At our study sites, common canopy tree species include *Betula platyphlla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurese*, *Acer mono*, and *Tilia amurensis*; beneath the tree species, the dominant shrubs are *Corylus mandshurica*, *Corylus heterophylla*, *Fructus schisandrae*, and *Acanthopanax senticosus*.

Study species

Mongolian oak, *Q. mongolica*, is native to eastern Asia and grows at moderate altitudes. It is a medium to large tree (10–20 m in height, with 0.5–1.0 m trunk in diameter) forming an open, somewhat irregular crown at maturity. Mongolian oaks produce large acorns with an average fresh mass of 4.40± 0.51 g (Yi and Zhang 2008a). Acorns usually fall between late August and mid-September. As an important food supply, acorns of Mongolian oak are dispersed and predated by small rodents and birds (Miyakia and Kikuzawa 1988). Acorns used in this study were collected from 30 oak trees with seed traps during the period of seed fall to make composite samples and incorporate variations in seed characteristics. Siberian chipmunk (*Tamias sibiricus*), a dominant diurnal rodent species in the Xiaoxing'an Mt region (Jin et al. 2004), consume, disperse, and scatter-hoard seeds of several local tree species (Yi and Zhang 2008b). Siberian chipmunks strongly depend on cached food for over-winter survival (Jin et al. 2004). Semi-natural enclosure investigations indicate that Siberian chipmunks are the most important rodent species scatter-hoarding acorns of *Q. mongolica* (unpublished data). In mid-September 2009, healthy adult Siberian chipmunks were field-captured and transported to animal care facilities within about 30 min after capture. No pregnant or lactating females were caught because field trapping was carried out at the end of the reproductive season. Animals were maintained individually in steel frame cages (H×W×L=90 cm×40 cm×50 cm) at ambient room temperature (day 15–20°C, night 10–15°C) and natural photoperiod (about 14 light hours). They were provided with carrots, peanuts, tree seeds collected from the local forests, and water ad libitum. No animals died during field trapping and laboratory procedures. A total of 16 healthy adult Siberian chipmunks were used for conducting experiments in semi-natural enclosures after being kept in captivity for 1 week for acclimation to captivity. Following behavioral experiments (approximately 1 week), all animals were released at the original sites of capture. Animals were handled with the permission of Henan University of Science and Technology.

Establishment of enclosures

Sixteen separate semi-natural enclosures (10 m×10 m) were established in an open and level area. The enclosures were built using bricks about 2.5 m high above ground and 0.5 m deep. The walls of the enclosures were smoothed to prevent escape of Siberian chipmunks. To prevent predators from entering the enclosures from outside, the enclosures were covered with plastic nets on the top. An artificial nest constructed of bricks (H×W×L=20 cm×15 cm×30 cm) and a plastic water bowl were placed in one corner of the enclosure to allow animals to rest and drink freely. A seed station of 0.5 m^2 was established at the center of each enclosure.

Experimental protocols

To test the first prediction, we provided each of 16 Siberian chipmunks with ten pairs of germinating and non-germinated *Q. mongolica* acorns. Germinating acorns were identified as those with a ≈1-cm-long radicle, while non-germinated acorns showed no radicle poking through the pericarp. A hole, 0.3 mm in diameter, was drilled far from the embryo of each acorn, then a flexible plastic tag (2.5 cm×3.5 cm, <0.3 g) was tied through the hole in each acorn using a thin 10-cm-long steel thread (Zhang and Wang 2001). Each tag was consecutively and discriminatively numbered to allow all acorns to be easily relocated and identified. When small rodents buried acorns in soil, shallow holes, or tree leaf litter, the tags were often left on the ground surface. Acorns were supplied to each individual at 7:00 AM. The tagged acorns in the enclosures were checked in the afternoon (16:00 PM). Seed fates were defined as intact in situ (IS), eaten in situ (EIS), eaten after removal (EAR), intact after removal (on surface) (IAR), and scatter-cached after removal (in soil) (CAR). We also recorded the number of acorns removed and cached to see which type of acorns (germinating or non-germinated) was preferred by Siberian chipmunks. Germinating acorns in caches were checked if their radicles and embryos were pruned or removed.

To test the second prediction, we continuously provided each Siberian chipmunk with to-be-germinated *Q. mongolica* acorns in semi-natural enclosures. The radicles of these acorns were expected to protrude through the pericarp in the following morning (day 1). On the first night (day 0), we released 30 to-be-germinated acorns at the center of each enclosure. Each acorn was consecutively and discriminatively numbered to allow all them to be easily identified. One individual of Siberian chipmunk was introduced into each enclosure at 7:00 AM on day 1. In the afternoon, seed fates, germination status, and radicle pruning of acorns were recorded. In the following three nights, we continuously added 30 to-be-germinated acorns to each enclosure to maximize survival probability of previously cached acorns, allowing cache management of chipmunks. Acorns cached each day were routinely checked if they were radicle-pruned or repeatedly pruned in the afternoon (days 2, 3, and 4). To explore if Siberian chipmunks prune long radicles and eat trimmed radicles, we presented each Siberian chipmunk with 20 acorns poking radicles ranging from 1 to 6 cm in length.

To test if Siberian chipmunks repeatedly prune radicles of *Q. mongolica* acorns in the field, we released 2,240 acorns in 112 seed stations with 20 acorns each in September 2009. Following the previous study (Zhang and Wang 2001), we marked the acorns with a 10-cm steel thread and a 3.5× 2.5 cm numbered plastic tag at the end. After removal, the cached acorns were located by surveying the areas around seed stations for tags protruding from the soil. Because Siberian chipmunks cache acorns only after the pericarp is totally removed in the study site (unpublished data), it is easy to identify caches made by Siberian chipmunks. For cached acorns by Siberian chipmunks, they were carefully checked to identify whether the radicles were pruned, and then recovered to keep the disturbance to a minimum (Xiao et al. 2009). During the following visits, we also checked the acorns in caches relocated in previous visits to see if the radicles are repeatedly pruned until they were excavated by Siberian chipmunks and/or other animals.

To find out whether radicle pruning stops or postpones acorn germination as stated in the third prediction, we carried out another experiment in which 25 germinating acorns with ≈1-cm-long radicle were pruned and another 25 non-germinated acorns were treated as control. Pruning involved cutting off the radicle poking through pericarp but maintaining the other embryonic parts in the same way as Siberian chipmunks did. All acorns were shelled because Siberian chipmunks always remove their pericarp before caching them (unpublished data). Imitating the way Siberian chipmunks cache the acorns, we buried two types of acorns into artificial caches on 10 transects (five acorns each) free from predation of animals and birds. Two weeks later, we checked whether they re-sprout (for radicle-pruned acorns) or germinate (for control acorns) and recorded the germination rates and radicle length. If radicle pruning failed to stop germination, we then pruned the radicles of all acorns and re-buried them in the caches. Another 2 weeks later, we checked how many radicle-pruned acorns re-sprout and recorded the length of radicles to see if repeated pruning slows down or postpones growth of radicles.

Statistics and analysis

Statistical Package for the Social Sciences (SPSS 16.0) was used for data analyses. A paired-samples T test was used to detect the difference in preference of Siberian chipmunks for non-germinated against germinating acorns in semi-natural enclosures. Levene's test was used to check for homoscedasticity and then independent samples T test or nonparametric T test was applied to explore the difference in the germination rates or radicle length between the control and pruned acorns. Differences in the proportions of cached acorns in the semi-natural enclosures in the consecutive 4 days were tested using General Linear Model (GLM), following arcsine transformation. The error distribution was specified using Levene's test. If the error variance is equal, LSD test was used; otherwise, Tamhane test was applied.

Results

Our results indicated that non-germinated *Q. mongolica* acorns were more likely to be removed than germinating ones by Siberian chipmunks from seed stations (t=2.300, df=15, P=0.036) (Fig. 1). However, the proportion of cached acorns did not differ significantly between the two types of acorns (t=−1.513, df=15, P=0.151) because more non-germinated acorns were eaten.

Regardless of consecutive addition of acorns for four times, Siberian chipmunks tended to select newly added non-germinated acorns and reject previous ones (most were germinated). Totally, 1.36% of acorns released in the previous days were removed in the following days, which can be seen from the same proportion of IS in the four acorn addition trials (GLM, F=0.087, df=3, P=0.996) (Fig. 2). Similarly, no difference was found in the proportion of CAR; however, the percentage of radicle-pruned acorns in caches increased with each addition of new acorns (from 34.21%, 43.40%, 75% to 97.06%, Fig. 3). Nevertheless, the percentages of radicle-pruned acorns in caches seemed to be similar at the end of experiments (71.05%, 80%, 83.33%, and 97%, Fig. 3), indicating that Siberian chipmunks actively participate in cache management. Our results clearly demonstrated that Siberian chipmunks pruned radicles of germinating acorns but did not excise embryo of either germinating or non-germinated acorns before caching. We found that some radicle-pruned acorns in the first day were re-pruned in the third and fourth day. Our results also showed that Siberian chipmunks pruned radicles of germinating acorns regardless of the length of radicles. However, they left trimmed radicles at the seed stations without eating them.

Our results showed that most radicle-pruned acorns continued developing radicles, as did the control group (Table 1). Removal of 1-cm-long radicle did not significantly influence germination rates (t=−0.577, df=8, P= 0.580) and radicle length (t=0.973, df=44, P=0.336). By removing acorn radicles, Siberian chipmunks could not cut off the flow of stored reserves from cotyledons to taproots. Although repeated pruning of radicles by chipmunks did not influence re-sprouting rates (t=1.116, df=8, P=0.297), it significantly slowed down the growth rates of newly sprouted radicles (F=63.35, df=1, P<0.001). Re-sprouting rates of acorns with longer radicles (mean=3.18 cm) were not affected by radicle pruning (t=−0.405, df=8, P=0.696); however,

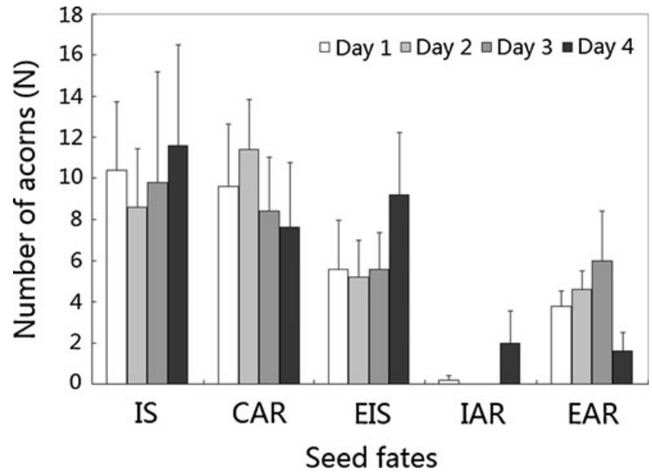

Fig. 2 Acorn dispersal of *Q. mongolica* by Siberian chipmunks in the semi-natural enclosures. Seed fates of the released acorns were measured as intact in situ (*IS*), eaten in situ (*EIS*), eaten after removal (*EAR*), intact after removal (on surface) (*IAR*), and scatter-cached after removal (in soil) (*CAR*). Data are expressed as mean±SD

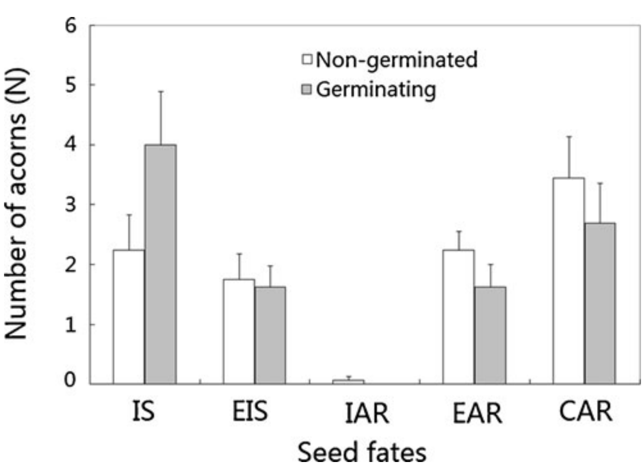

Fig. 1 Preference of Siberian chipmunks for germinating and non-germinated acorns of *Q. mongolica*. Data are expressed as mean±SD

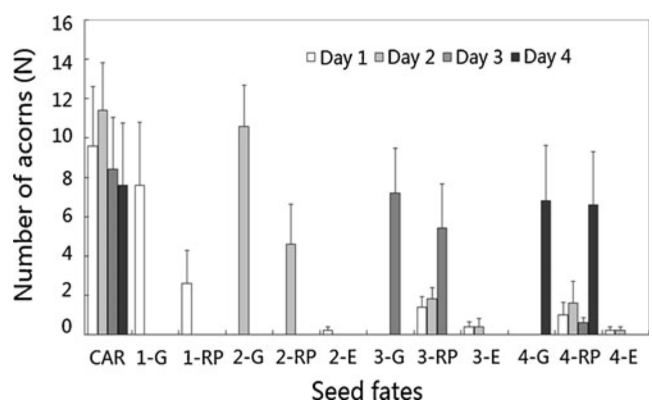

Fig. 3 Radicle pruning of *Q. mongolica* acorns by Siberian chipmunks in the semi-natural enclosures. Data are expressed as mean±SD. *1-G*, *2-G*, *3-G*, and *4-G* indicate the number of germinated acorns in days 1, 2, 3, and 4, respectively; *1-RP*, *2-RP*, *3-RP*, and *4-RP* represent the number of radicle-pruned acorns in days 1, 2, 3, and 4, respectively; *2-E*, *3-E*, and *4-E* refer to the number of acorns eaten by Siberian chipmunk in days 2, 3, and 4, respectively

Table 1 Effect of radicle pruning on germination rates and taproot length of *Q. mongolica* acorns

Acorn type	Germination rate (%)	Taproot length (cm)
Control	88.00±10.95	3.18±1.44
Radicle-pruned	92.00±10.95	2.79±1.28
Repeated pruning	79.00±14.30	0.46±0.23
Pruned “control”	91.00±12.45	0.83±0.43

Data are expressed as mean±SD

the growth rates of radicles were significantly postponed (F=49.615, df=1, P<0.001).

In the field experiment, we located 173 scatter-hoarded acorns by Siberian chipmunks in total, of which 116 acorns were excavated by Siberian chipmunks or other small rodents before germinating; 57 acorns in caches were radicle-pruned and 43 acorns were pruned more than once. These results suggest that the deliberate behavior of radicle pruning would be a cache management of Siberian chipmunks. Although germinating acorns in caches were radicle-pruned and re-cached more than once, 96.7% of them were recovered or consumed within 20 days. However, 15.4% cached acorns with pericarp remained in caches made by other small mammals.

Discussion

If the behavior of radicle pruning is a requirement for preventing loss of food reserves to seedlings, one would expect that Siberian chipmunks prefer to cache non-germinated acorns rather than germinating ones, and hence need less investment in surveillance and interventions when caching. However, Siberian chipmunks equally scatter-hoarded the two types of acorns in the semi-natural enclosures, falsifying the first prediction. No difference in the proportions of non-germinated and germinating acorns in caches can be explained by the high efficiency of cache management of chipmunks. However, we noticed that chipmunks preferred to select non-germinated acorns for caching in the acorn addition experiments. This discrepancy could be explained by the frequency-dependent effect that non-germinated acorns outnumber the germinating ones (Xiao et al. 2010).

Our results indicated that Siberian chipmunks actively pruned the radicles of germinating acorns of *Q. mongolica* before caching and re-prune them after caching both in field and semi-natural enclosures, regardless of the length of the radicles. However, this behavior was different from embryo excision performed by tree squirrels, which also prevents autumn germination of nondormant seeds (Fox 1982; Steele et al. 2001a). Embryo excision of white oak species by several species of *Sciurus* has been well documented in North America (Fox 1982; Steele et al. 2001a, b 2006; Steele 2008), whereas no other rodent species are found to excise the embryo of white oak acorns, although many of them are sensitive to germination schedules. Xiao et al. (2009, 2010) recently reported the behavior of embryo excision by Pallas's squirrel (*Callosciurus erythraeus*) and Père David's Rock squirrel (*Sciurotamias davidianus*) in Asia, implying a convergent evolution tactic to counter acorn germination among squirrel species across different continents. Although there are few studies that document re-visitation of scatter hoards (Vander Wall and Joyner 1998), Siberian chipmunks were found to prune radicles of some cached acorns for more than once in our study, displaying a deliberate behavior of cache management. To our knowledge, this would be the first study show that scatter-hoarding animals revisit and manage their caches through radicle pruning. Despite lower efficiency in stopping acorn germination than embryo excision, repeated radicle pruning could be regarded as a cache management tactic of Siberian chipmunks. Siberian chipmunks frequently and repeatedly pruned the radicles rather than removed the embryos of white oak acorns in our study, suggesting that the behavior of radicle pruning has replaced that of embryo excision in chipmunks. Squirrels and chipmunks may have evolved different tactics to cope with fast germination of acorns of white oak species.

The third prediction that radicle pruning prevents germination of acorns was partially supported in our study. Pruning of short radicles did not significantly slow down the acorn germination rates or stop the conversion of energy from cotyledons to taproots. However, repeated pruning and removal of longer radicles significantly postponed re-sprouting and growth of the radicles. These results are in agreement with other studies that seed germination is prevented or delayed by manipulation of rodent species (Elliott 1978 Jansen et al. 2006; Xiao et al. 2009), indicating that Siberian chipmunks actively manage their caches by pruning the radicles of germinating acorns. However, repeated radicle pruning seemed to be not fatal to *Q. mongolica* acorns, echoing the previous results that radicle pruning has almost no effect on seedling performance (Bonner 1982; Barden and Bowersox 1989; McCreary 1996; Cicek et al. 2006; Tilki and Alptekin 2006). Hence, the radicle-pruned acorns in caches are expected to have an opportunity to germinate in the following year provided they are not excavated by rodents.

Siberian chipmunks discarded radicles after pruning them from acorns, suggesting that pruning was not for eating radicles (Smith and Follmer 1972; Fox 1982). Although repeated pruning helps delay acorn germination, it would be less economical for animals to prune re-sprouting radicles of acorns in caches several times. But the situation may be not true because chipmunks do not need to invest heavily in surveillance and interventions after acorns have been repeatedly pruned when temperatures are low, such as those occurring in mid-October. Conditions such as these will naturally postpone or stop re-growth of radicles. Furthermore, Siberian chipmunks excavated almost all scatter-hoarded acorns within 20 days. This seemingly indicates that Siberian chipmunks rely on *Q. mongolica* acorns as short-term reserves. Nevertheless, Siberian chipmunks hibernate in a permanent burrow with a food supply in winter (Jin et al. 2004). Therefore, Siberian chipmunks, like Eastern chipmunks (Clarke and Kramer, 1994) and Yellow pine chipmunks (Kuhn and Vander Wall 2009), are most likely to rely on scatter hoarding for rapid sequestering of seeds during seed fall but subsequently transfer them into their larders prior to hibernation. Hence, radicle pruning by Siberian chipmunks can be expected in their larders although we did not locate their dens. In this context, radicle pruning would be an evolutionary cache management tactic of Siberian chipmunks, supporting our last prediction.

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