Partial acorn consumption by small rodents: implication for regeneration of white oak, *Quercus mongolica*

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Abstract Partial consumption of acorns by rodents, birds, and insects has been widely reported in various oak species. However, to what extent these partially eaten acorns contribute to the regeneration of oak trees is poorly understood. To date, there is limited knowledge of the effects of seed availability on partial consumption of acorns. Herein, we released tagged *Quercus mongolica* acorns in two consecutive years with different seed crops, to explore the probability of partial acorn consumption. We also placed simulated partially consumed acorns in the field to investigate their contribution to regeneration of white oak. Our results showed that more acorns were partially eaten in a good crop year than in poor crop year, reflecting an effect of predator satiation on acorn partial consumption by rodents at the population level. Partially eaten acorns were more likely to be damaged at the basal end, suggesting consistent consumption preferences of small rodents. Although, partially consumed acorns were less likely to be scatter-hoarded by small rodents, they germinated more rapidly than the intact acorns in the field, offsetting the negative effects of the non-buried deposition. Despite lower germination rates, lightly damaged acorns exhibited greater growth of roots and shoots, suggesting a compensatory response to partial acorn consumption. Partial consumption may spread predation pressure on acorns and thus appears to be much better for the plant than total consumption by seed-eating animals. Therefore, partially consumed acorns as dispersal leftovers may play a potential role in natural regeneration of *Quercus mongolica*, especially in mast years. However, this role and the underlying mechanisms of partial acorn consumption by rodents, birds, and herbivore insects need further investigation.

Keywords Acorn · Partial consumption · Cotyledon loss · Seed dispersal · Seedling establishment

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Introduction

Acorns of oak species contain a large amount of nutritional reserves in their cotyledons (Short 1976; Servello and Kirkpatrick 1987). Consequently, seed predators (e.g., rodent and bird) rely on these resources for survival and reproduction (Mellanby 1968; Shaw 1968; Borchert et al. 1989; Maetô 1995; Den Ouden et al. 2005). Plants bearing large-sized seeds, however, have evolved a number of morphological, physical, and chemical adaptations to defense against many kinds of seed-eating animals (Zhang and Maun 1991;

Steele et al. 1993; Xiao et al. 2007; Yi and Yang 2010a, b). Three mechanisms can be attributed to plant's defenses against predation by animals: resistance, tolerance, and avoidance (Fineblum and Rausher 1995; Siemens et al. 2003; Xiao et al. 2007). Partial consumption of large seeds has been reported for many plant species across temperate and tropical ecosystems to tolerate seed predation (Steele et al. 1993, 1998; Ollerton and Lack 1996; Vallejo-Marín et al. 2006; Xiao et al. 2007; Dube et al. 2010; Yi and Yang 2010a, b), and is supposed to be a consequence of chemical and/or morphological defenses of plants. This adaptation of acorns is widely interpreted as large-sized seeds with a high tannin concentration in the apical part (Steele et al. 1993; Bonal et al. 2007).

Although loss of nutritional reserves caused by partial seed predation exerts negative effects on seed germination and seedling performance (Westoby et al. 1992; Bonal et al. 2007; Hou et al. 2010), it has been widely demonstrated that partially eaten acorns can germinate and develop into normal seedlings provided the vulnerable embryonic parts successfully escape predation of animals (Andersson and Frost 1996; Branco et al. 2002; Xiao et al. 2007; Pérez et al. 2008; Hou et al. 2010; Yi and Yang 2010a; Perea et al. 2011a). Therefore, partial consumption of acorns may play an alternative role in shaping seed dispersal patterns and oak regeneration processes. However, the prerequisite for seedling establishment from partially eaten acorns is the suitable environments for them to germinate. Although gray squirrels regularly cache apical fragments of red oak (Quercus rubra) acorns after partial predation (Steele et al. 1998), rodents and blue jays tend to drop the partially eaten acorns on the ground rather than cache them (Moore and Swihart 2006; Perea et al. 2011a). Whether the partially consumed acorns dropped by animals can germinate in the field still remains uncertain, although they can successfully germinate and survive in germination chambers containing peat and perlite (Perea et al. 2011a).

To our knowledge, partial consumption of the basal end of acorns by animals has mainly found in the section of Lobatae, Cerris, and Mesobalanus in subgenera of Quercus (Steele et al. 1993, 1996, 1998; Dunning et al. 2002; Hou et al. 2010; Perea et al. 2011a; Yi and Yang 2010b); there are few reports on white oak species (section Quercus) (Yi and Yang 2010a). Our field observations indicate that wood mice and Siberian chipmunks selectively consume the basal

portion of Quercus mongolica acorns, and the partially consumed acorns are more frequently left on the surface rather than cached, especially in the mast years. Seeds in caches are usually recovered by hoarding animals or pilfered by competitors (Vander Wall 1990); however, partially consumed acorns left on the ground can be regarded as a leftover by animals (Perea et al. 2011a), which may have a lower probability of predation by rodents than the cached acorns. In addition, acorns on the ground are more likely to be exposed to desiccation, frosts, or other microbial agents (see Lambert 2002; Perea et al. 2011b). Although repeated movement of seeds is common and increases partial consumption, little is known about the ecological role of partially consumed acorns in contributing to regeneration of oak species (Perea et al. 2011a).

Mast seeding has been recognized to generate a "predator satiation" effect on seed-eating animals (Kelly 1994; Crawley and Long 1995; Kelly and Sork 2002). Consequently, more partially eaten acorns can be expected due to high seed availability. To date, there is limited knowledge of acorn partial consumption at different levels of seed abundances; although large acorns are more likely to be partially eaten than small ones at individual level (Yi and Yang 2010a; Perea et al. 2011a). Therefore, it is necessary to explore partial consumption of acorns by animals and its ecological role in seedling establishment with regard to seed abundance. Herein, we released tagged acorns of Q. mongolica in two consecutive years with different acorn crops and tracked the relationship between acorn partial consumption and seed availability. In addition, we placed artificially cut acorns in enclosures in the field to examine the effects of partial consumption on germination and seedling establishment. We also attempted to assess the ecological implications of partial acorn consumption in the natural regeneration of Q. mongolica.

Materials and methods

Study areas

This study was conducted in September 2009 and 2010 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. Average 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 platyphylla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurense*, *Acer mono*, and *Tilia amurensis*. Beneath the tree species, the dominant shrubs are *Corylus mandshurica*, *C. heterophylla*, *Fructus schisandrae*, and *Acanthopanax senticosus*.

Study species

Mongolian oak, *Quercus mongolica*, is native to eastern Asia and grows at moderate altitudes. It is a medium to large tree (10−20-m height, with 0.5–1.0-m trunk 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 2008). As an important food supply, acorns of *Q. mongolica* are dispersed and eaten by small rodents and birds (Miyaki and Kikuzawa 1988; Yang et al. 2011). Acorns of *Q. mongolica* usually fall between late August and mid-September. In this study, the average acorn crop was estimated using seed traps. Thirty seed traps deployed in an area of 40,000 m^2 were used to measure seed fall under 30 oak trees. Seed traps, excluding terrestrial vertebrate predators, were designed to capture acorns. A seed trap was made of a 1 m × 1.2 m polyester net (2-mm mesh) on a 0.5-m^2 metal frame. The frame was set on a thin wooden rod about 1.5 m above the ground to prevent predation by terrestrial vertebrates. Traps were established to catch acorns and other debris while letting rainfall easily pass through. One seed trap 1–2 m away from each tree trunk was randomly placed under each of the crown of the selected oak trees just before acorns ripened. Traps were left in place until all acorns had fallen from the trees. Avian predation is regarded to be of little influence on potential losses of acorns because few bird species are witnessed in the experiment sites during our survey, most of them are small-sized passerines unable to swallow the acorns.

Chemical compositions of the apical and basal parts of *Q. mongolica* acorn

To explore if there were differences in chemical compositions between the apical and the basal parts of *Q. mongolica* acorns, we selected 100 sound acorns from several trees and randomly sorted them into five groups with 20 acorns per group. For each group, acorns were cut into half transversely and the apical or basal parts were pooled for chemical analyses. Concentrations of crude protein, crude fat, crude starch, and tannins were measured by the Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences (No.12, Southern Zhongguancun Road, Haidian District, Beijing).

Acorn dispersal by rodents

We witnessed an extreme failure of acorn crops of *Q. mongolica* in 2007, 2008, and 2011. It was a poor year of *Q. mongolica* acorns in 2009 but a large crop year in 2010 in the study area, showing a synchronous, episodic production of heavy acorn crops by *Q. mongolica*. All the *Q. mongolica* acorns were collected in the study area from 10–15 oak trees during the period of seed fall, to make composite samples and incorporate variations in seed sizes. During seed fall in 2009 and 2010, we released 400 and 440 sound acorns into 20 and 22 seed stations, respectively. For acorn tagging, 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 (Yi and Zhang 2008). Each tag has a unique identity to allow all the acorns to be easily relocated and identified. When small rodents bury acorns in the soil, shallow holes or litter, the tags are often left on the ground surface. After seed placement, we searched the area around each seed station (radius <20 m) every day for 10 days to determine fates of acorns. Two observers each searched the area around each seed station for 20 min in both years of the study. The seed fates were sorted into six categories: (1) intact in situ (IS); (2) eaten in situ (EIS); (3) eaten after removal (EAR), (4) intact after removal (on surface) (IAR); (5) cached after removal (in soil) (CAR); and (6) missing (perhaps larder-hoarded in burrow or not seen) (M). For the category of EAR, we further divided it into three groups: complete consumption (only pericarp
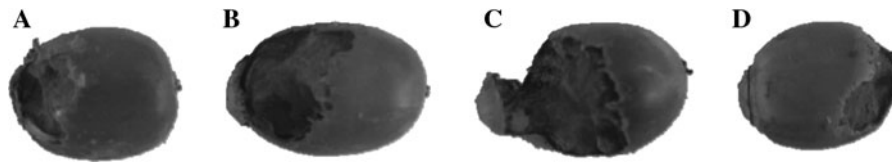
Fig. 1 Leftovers by small rodents in dispersal of *Quercus mongolica* acorns. Apical end of the acorn refers to the part containing the embryo, whereas the basal end refers to the

opposite part of the acorn. Shown are basal (**a–c**) and apical (**d**) partial consumption of *Quercus mongolica* acorns

debris left), basal consumption (teeth marks found on the basal half the acorn), and apical consumption (teeth marks found on the apical half the acorn) (Fig. 1). We also checked if partially eaten acorns were cached by small rodents in their scatter hoarders. In the next spring, tagged acorns in caches and partially eaten acorns were checked to determine whether they had germinated into seedlings.

Acorn release for germination

In autumn 2010, 300 sound acorns were selected and randomly divided them into three groups with 100 acorns per group. One group was treated as control, and the other two groups were cut-off half (half-loss group) or one-fourth (quarter-loss group) of the acorn length, respectively, to simulate heavy and slight consumption by small rodents. In autumn, we established five enclosures (1 m × 1 m × 0.4 m) with steel net frame in natural conditions free from predation of rodents. Then, 20 acorns of each group were randomly placed in each enclosure 10-cm apart. To imitate the deposition of partially consumed acorns left on the ground by small rodents, we covered the acorns with 1–2 leaves of *Q. mongolica*. Germinated acorns were defined those with taproot penetrating into the soil. Germination rates were measured every day after placement for 15 days. Seedling survival, seedling height, leaf number, root length, and dry weight of root and shoot biomass were measured in the next year.

Data analysis

Statistical Package for the Social Sciences (SPSS 16.0) was used for data analysis. Mann–Whitney *U* test was used to detect the difference in the acorn crops in 2009 and 2010. Differences in the number of acorns with different seed fates between 2009 and 2010 were tested using General linear model. We used

Chi-square test to see if there was difference between the proportion of partially eaten acorns between 2009 and 2010. Time to germination was evaluated using a General linear model repeated measures test. Chi-square test was used to test the difference in the final germination rates. Paired-samples *T* test was used to test if there were differences in chemical compositions between apical and basal parts of acorns.

Results

Acorn partial consumption in response to seed availability

Our study showed that acorn crop of *Q. mongolica* in 2010 was larger than that in 2009 (26.67 ± 10.22 vs. 6.20 ± 2.09 acorns/m^2) (Mann–Whitney *U* test: $Z = -2.166$, $P = 0.030$). There was a higher percentage of weevil infestation in 2009 (34.78%) than in 2010 (3.96%). We found no difference in the tannin concentration and nutrition reserves between the apical and the basal ends of *Q. mongolica* acorns (Fig. 2). More acorns were remained at seed stations in 2010 (24%) than in 2009 (1.25%) ($F = 27.803$, df = 1, $P < 0.001$) (Fig. 3). However, a larger proportion of acorns were
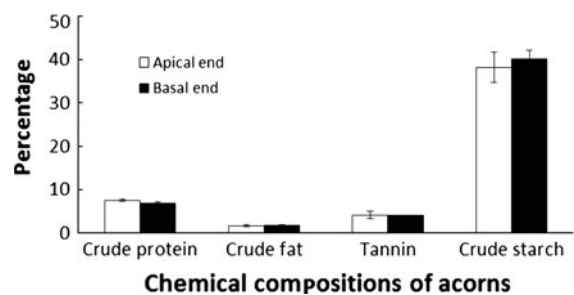

Fig. 2 Differences in chemical composition between the basal and the apical ends of *Quercus mongolica* acorns. Data are expressed as mean ± SD
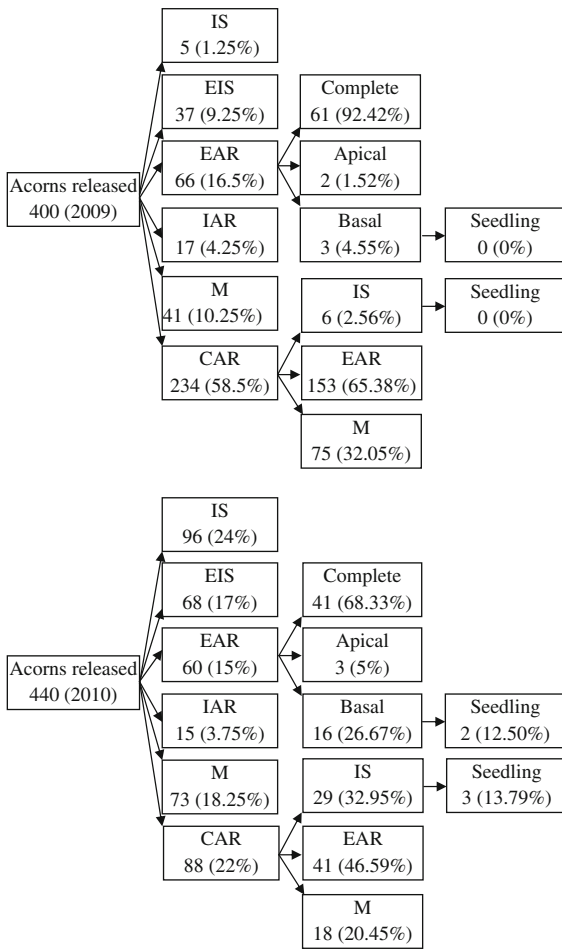
Fig. 3 Acorn fates exposed to small rodents in 2009 and 2010 in the field, showing the percentages and number of *Quercus mongolica* acorns with different fates. IS, EIS, EAR, IAR, CAR, and M represent acorns intact in situ, eaten in situ, eaten after removed, intact after removed, cached after removed, and missing, respectively. Of the EAR acorns, complete consumption was identified as those that only pericarp debris were left; basal consumption refers to the partially eaten acorn that teeth marks were found on the basal half, and apical consumption refers to the partially eaten acorn that teeth marks were found on the apical half (see Fig. 1)

scatter-hoarded in 2009 ($F = 32.820$, df $= 1$, $P < 0.001$). No difference in the proportion of acorns eaten after removal (EAR) was detected between 2009 and 2010 ($F = 2.753$, df $= 1$, $P = 0.105$) (Fig. 3), however, more acorns were partially consumed (at the basal end) in 2010 than in 2009 (26.67% vs. 4.55%, $\chi^2 = 15.125$, df $= 1$, $P < 0.001$) (Fig. 3), suggesting that a high level of seed abundance facilitates partial

consumption of acorns. Of the partially eaten acorns, 60% (3/5) and 84.21% (16/19) of them were found damaged at the basal end in 2009 and 2010, respectively, indicating that small rodents show a consistent preference for partial consumption of the basal end of *Q. mongolica* acorns (Fig. 3). However, a very small proportion of acorns in scatter caches were observed to be partially eaten by rodents both in 2009 and in 2010, suggesting that rodents tend to avoid caching partially consumed acorns. Seedlings were not found from cached acorns or from partially eaten acorns in 2010. However, two seedlings germinated from partially eaten acorns and three from cached acorns in 2011.

Germination and seedling establishment from partial eaten acorns in the field

GLM repeated measures test revealed that time to germination was significantly affected by artificial partial consumption ($F = 11.178$, df $= 2$; $P = 0.001$) (Fig. 4). Time to germination during the first 9 days was accelerated in both half- and quarter-loss groups compared with the intact acorns ($P = 0.015$, $P = 0.002$). However, no difference was detected between the half- and quarter-loss groups ($P = 0.767$) (Fig. 4). The final proportion of acorns that germinated was significantly affected by partial consumption ($\chi^2 = 7.470$, df $= 2$, $P = 0.024$), with the half-loss group exhibiting the lowest germination rate (78%, 59%, and 48%, respectively) (Fig. 4). Root length was found to be significantly affected by partial consumption ($F = 11.639$, df $= 2$, $P < 0.001$) (Fig. 5a). Multiple comparisons indicated that the quarter-loss group exhibited the longest root length than the intact ($P = 0.004$) and
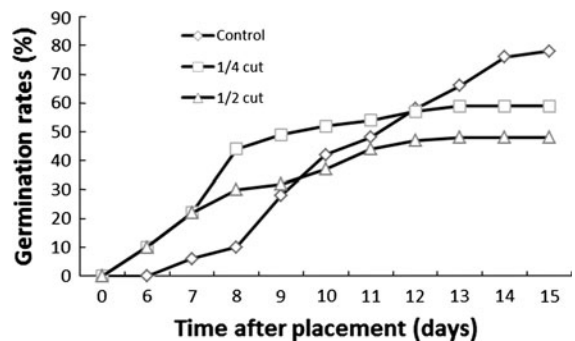

Fig. 4 Germination dynamics of *Quercus mongolica* acorns after placement in enclosures in the field
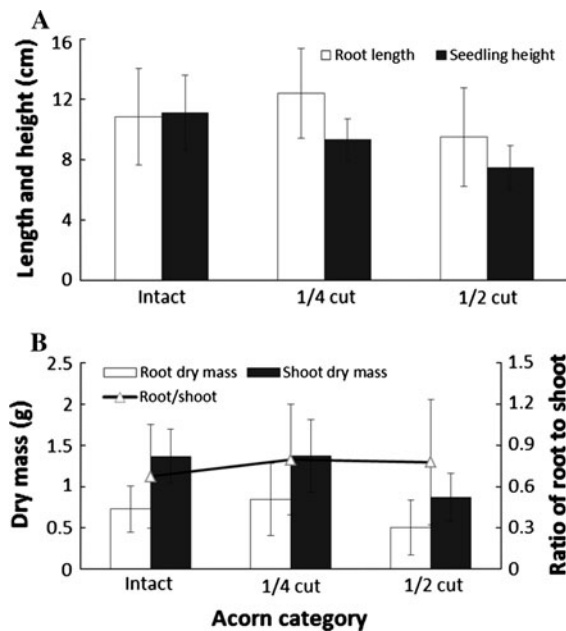
Fig. 5 Root length, shoot height, root dry mass, shoot dry mass, and ratio of root to shoot of seedlings of *Quercus mongolica* from partially consumed acorns. Data are expressed as mean ± SD

half-loss groups ($P < 0.001$). Root length of the intact acorns was also longer than that of the half-loss group ($P = 0.022$) (Fig. 5a). Root biomass was also significantly affected by the degree of acorn damage ($F = 11.639$, df = 2, $P < 0.001$) (Fig. 5b), with the half-loss groups significantly lower than the intact and the quarter-loss groups ($P = 0.001$, $P < 0.001$), respectively. However, there was no difference in root mass between the intact and the quarter-loss groups ($P = 0.225$) (Fig. 5b). Partial consumption significantly decreased seedling height ($F = 29.250$, df = 2, $P < 0.001$) (Fig. 5a). Seedlings from the intact and the quarter-loss groups were taller than those from the half-loss group, respectively (all $P < 0.001$). Simulated acorn consumption significantly affected shoot biomass ($F = 19.873$, df = 2, $P < 0.001$) (Fig. 5b). Shoot biomass was significantly lowered by half-loss of cotyledons compared with the intact and the quarter-loss groups (all $P < 0.001$). However, the intact and the quarter-loss groups showed no differences in shoot biomass ($P = 0.135$) (Fig. 5b). The ratio of root to shoot was not significantly influenced by simulated partial consumption of acorns ($F = 1.111$, df = 2, $P = 0.333$) (Fig. 5b).

Discussion

Acorn partial consumption

Previous studies accumulate that acorn damage by rodents, birds, and even insects are often found at the basal end far from the vulnerable embryo of the propagules (Bossema 1979; Steele et al. 1996, 1998; Bonal et al. 2007; Xiao et al. 2007; Perea et al. 2011a; Yi and Yang 2010b). In agreement with these results, most of the seed damage caused by partial consumption was found at the basal end of *Q. mongolica* acorns in our study. This partial consumption preference has long been explained by the unbalanced distribution of tannins in seeds, seed geometry, seed size, or pericarp thickness (Steele et al. 1993, 1998; Bonal et al. 2007; Hou et al. 2010; Yi and Yang 2010b). More recently, Steele and his colleagues found that both lipid and Na levels are significantly higher in the basal end than the apical portion of the acorns of three additional oak species (Steele and others, unpublished data), which are vital to herbivorous mammals such as tree squirrels (Steele and Koprowski 2001). However, when acorns are carved to reverse the basal and apical ends, tree squirrels begin eating from the true apical end of the seed where tannin level is higher and lipid lower (Steele et al. 1998). It is likely that partial consumption cannot be explained by the tannin concentration and nutrition reserves between the apical and basal ends of *Q. mongolica* acorns. Acorn chemistry and seed size are not plausible explanations for basal partial consumption; although, there may be a high concentration of tannin at the very apex of the acorn or some other deterrent compounds may distribute differently in the apical and the basal ends. Weevil infestation is very common and usually causes severe damage to the *Quercus* acorns (Oak 1993; Dunning et al. 2002; Bonal et al. 2007; Xiao et al. 2007; Yi and Yang 2010a, b). However, weevil infestation is frequently found at the basal end of acorns (Steele et al. 1996; Branco et al. 2002; Dunning et al. 2002; Hou et al. 2010; Yi and Yang 2010a, b). Weevil infestation may be also manipulated by the unbalanced distribution of these secondary compounds, whereas, recent studies show that differential thickening of acorn epicarp of *Quercus variabilis* is responsible for the partial consumption of basal parts by weevil larvae (Yi and Yang 2010b). Artificial cutting demonstrates that slight damage to the apical part usually causes acorn

death, reflecting that the apical end of acorn is far more important than the basal end in supporting seed viability (Hou et al. 2010). Therefore, coupling with these facts, we argue that preferential consumption of the basal portion of acorns results from rodents foraging for insect larvae in the basal portion. Although we lack direct evidence, small rodents may attempt more acorns to find weevil larvae for protein supply and then abandon them in 2010 when energy resources are not limited, resulting in more partially consumed acorns than in 2009. High level of seed abundance seems to facilitate partial acorn consumption of *Q. mongolica* acorns by small rodents. This may be a modified form of the "predator satiation" that has been described elsewhere for large seed crops (Janzen 1971; Crawley and Long 1995). We found an equal proportion of seedlings from cached acorns and partially eaten acorns in 2010 with high seed abundance, further highlighting the important role of acorns partial consumption in supporting oak regeneration, especially in mast seeding years.

Germination of partially eaten acorns

Our study clearly showed that the partially consumed acorns germinated more rapidly than the intact ones, well in agreement with previous studies on *Quercus* sp. (Fukumoto and Kajimura 2000; Branco et al. 2002; Hou et al. 2010; Perea et al. 2011a). This germination pattern of partially consumed acorns can be explained by some physiological responses to seed damages (Vallejo-Marín et al. 2006; Pérez et al. 2008). Faster water uptake from a section made by cut-off treatments would be expected in partially cut acorns (Kikuzawa and Koyama 1999). This can also be explained by the fact that herbivory damage to seeds can induce faster export from edible tissues and greater partitioning into tissues inaccessible to foraging herbivores (Orians et al. 2011). More rapid germination and translocation of cotyledon reserves to root or shoot may lead seedling to emerge faster above the ground and to produce hydrocarbons by photosynthesis in earlier season, suggesting one compensatory response to partial cotyledonary herbivory. However, the final germination rates of the partially consumed acorns were significantly lower than those of the intact acorns, similar to Hou et al. (2010) but different from Steele et al. (1993) and Andersson and Frost (1996) who have reported that

cotyledon extirpation had less effect on seedling growth of oaks. Our results are also consistent with the effects of cotyledon excision on seedling establishment (Andersson and Frost 1996; Frost and Rydin 1997; Milberg and Lamont 1997; Bonfil 1998; Branco et al. 2002). Although the germination rates were low, seedlings from the quarter-loss group exhibited the same performance to the intact acorns in terms of root and shoot biomass. However, heavy loss of cotyledons (half-loss group) not only significantly reduced the germination rates but also severely influenced seedling performance, indicating that few reserves are available for seedling growth due to loss of cotyledon reserves (Fukumoto and Kajimura 2000; Branco et al. 2002). The balance of shoot/root dry mass was slightly affected by partial consumption of acorns, similar to the results on *Q. suber* (Branco et al. 2002).

Implication for oak regeneration

Our study helps better understand the seed dispersal ecology of oaks and to evaluate the ecological role of partially consumed acorns in supporting seedling establishment and potentially affecting oak regeneration patterns. Partially consumed acorns, due to rapid germination, may be more likely than intact ones to escape post-dispersal predation by animals. This may serve as an alternative mechanism in seed dispersal of oak species. Seed availability exerts great influence on the probability of partial consumption of *Q. mongolica* acorns. Predator satiation effect under high level of seed abundance is expected to promote partial consumption of acorns, and to increase the possibility of seedling establishment from these leftovers. Although the possibility of partial consumption has been found to be related to seed size, seed geometry, and chemical traits, we should also consider the behavior of small rodents and birds foraging for insect larvae as a potential cause of partial seed consumption. Future studies should focus on exploring the nature and the ecology of partial acorn consumption by rodents, birds, and insects in response to acorn production in multiple years. More work should also concentrate on the effect of the partial seed consumption by animals on the seedling establishment and regeneration of oak species.

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