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Evidence on the Adaptive Recruitment of Chinese Cork Oak (*Quercus variabilis* Bl.): Influence on Repeated Germination and Constraint Germination by Food-Hoarding Animals

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Abstract: In drought temperate forest, seedling recruitment is highly dependent on seed burial by native animal dispersers. To prolong seed storage, animals often take measures to impede seed germination. Aiming to understand the strategic balance between the natural seed germination and the role played by animals in the constraint germination procedures, we investigated the stages on the germinated acorns of Chinese cork oak (*Quercus variabilis* Bl.) and the rodents' behavior on the consequential delay in developmental processes of acorns in Mt. Taihangshan area of Jiyuan, Henan, China. The results showed that (1) *Apodemus peninsulae* Thomas excise radicles from germinated acorns before hoarding; (2) radicle-excised acorns re-germinate successfully if the excised radicle was un-lignified, but reverse if excised radicle was lignified; and (3) seedlings derived from radicle-excised acorns produce more lateral roots than that of sound acorns. We conclude that rodents take the radicle-excision behavior as a deliberate mechanism to slow the rapid germination of acorns; nevertheless, the acorns adaptively respond to this negative treatment and counteract the constraint from rodents by regermination to preserve the viability of the seeds. Consequently, this plays a significant role in forest recruitment. This study proves the new survival model of Chinese cork oak against animal predation, and will broaden theories of animal-forest interaction, forest succession and can be used as a meaningful venture to temperate forest restoration efforts.

Keywords: temperate forest; radicle-excision; re-germination; lignification; seedling establishment

1. Introduction

Habitat loss is a primary cause of biodiversity decline [1], and forest restoration is an important remedial measure contributing to biodiversity conservation in forest ecosystems [2]. However, seedling recruitment and forest restoration are highly affected by some abiotic and biotic factors such as high predation on seeds by animals, periodic drought, soil degradation and lack of seed dispersal [3,4]. The key factors vary greatly among different species and areas [5].

Due to global climate change, drought is increasingly observed around the world, and this is becoming a fundamental threat to local forest regeneration [5,6]. Many forest seeds are sensitive to desiccation and temperature [7–9]. The low soil moisture is responsible for the drought stress in seed germination and also affects the seedling survival [3,10]. Burying the seeds in soil conserves their moisture for germination, and also creates a favorable environmental condition for the seedling establishment and recruitment in the forest [11–13]. The natural regeneration of larger-seeded animal-dispersed trees are mostly associated with seed burying by seed dispersers [5,9]. In temperate monsoon areas, the distribution of rainfall is highly erratic in seasonality, with the dry season possibly extending for several months during winter (December–February) and the next spring (March and April) [14,15]. This persistent seasonal drought becomes an important stress to forest regeneration [16,17].

The Chinese cork oak (*Quercus variabilis*), is a predominant white oak tree species found in central and south China and is also widespread in the Mt. Taihangshan area [18,19]. The seed production for this tree species exhibited a regular inter-annual fluctuation (Yifeng Zhang unpublished data). Oak seeds are nutritious for seed-eating animals, and serve as a favorable food resource for most seed hoarders [20–22]. Seeds of white oak have a short dormancy period and can germinate rapidly in a suitable environment [21,23,24]. This quick germination, characteristic of the oak seeds, deprives the food resource for hoarders because nutrients and energy of acorns would transfer rapidly from cotyledon into the radicle [25–27]. Moreover, the germinated seed develops into secondary materials, e.g., tannins [13], which are toxic to digestive organs and/or absorptive tissues such as gut epithelium, liver and kidney [28,29]. Therefore, some species of seed-hoarding animals often take management measures to prevent or delay seed germination, and radicles-excision is one of the common anti-germination measures in many of Sciuridae and Muridae species [30–33]. On the other hand, if radicle-excised seeds fail to continue sprouting, the forest regeneration will become gravely impeded.

Up to now, there is lack of information whether those radicles-excised seeds could germinate under suitable environmental conditions. In the current study, we intended to test the potential viability of acorns radicle-excised by rodents. In the field, we observed that some excised-acorns with young radicles can continue to develop, while those with mature radicle cannot. Thus, we predicted that the rodent-treated acorns would re-germinate if radicles were removed in the early developing stage. In contrast, acorns with radicles excised in the later growing period would lose their viability to germinate.

2. Methods and Materials

2.1. Study Area

This study was conducted in a temperate *Q. variabilis* secondary forest at State-Owned Yugong Forest Farm (600 m a. s. l., 35°08′ N, 112°16′ E) in Mt. Taihangshan area of Jiyuan, Henan, China. This area was controlled by continental monsoon climate, with an average annual rainfall of 600~700 mm and mean temperature of 14.3 °C. Vegetation in this region can be divided into three types: coniferous forest, broad-leaved forest and low shrubs. At our study site, common canopy tree species included: *Amygdalus davidiana* (Carr.) C. de Vos ex Henry, *Armeniaca sibirica* (Linn.) Lam., *Q. variabilis*, *A. persica* Linn., *Populus tomentosa* Carr., *Robinia pseudoacacia* Linn. and *Platycladus orientalis* (Linn.) Franco. The undergrowth species included: *Lespedeza bicolor* Turcz., *Cotinus coggygria* Scop. var. *pubescens* Engl., *Ziziphus jujuba* Mill. var. *spinosa* (Bge.) Hu ex H. F. Chow and *Rosa xanthine* Lindl. [18,34]. *Apodemus peninsulae* Thomas (23.90 ± 1.81 g in body mass) was one of the main acorn dispersers and predators in study area [18,19].

2.2. Seed Collection and Preservation

Acorns of *Q. variabilis* were collected in September and October 2010. The mean number of acorns per m^2 of canopy area was 7.08 in 2010, and this was a high seeding year. We chose 10 healthy adjacently located mother trees with similar growth patterns (e.g., diameter, canopy), for collection of seeds in fruiting season. When acorns matured and dropped to the ground, we gathered all the seeds every day and took them to the laboratory. The sound (undamaged by worms) acorns were selected and kept in PVC buckets, and then covered with trace-moisture sand to prevent acorns from dehydration and deterioration. The buckets were put in a refrigerator at 4 °C to prevent germination until used [35].

2.3. Animal Trapping

From March to April 2011, *Apodemus peninsulae* were live-trapped using steel-wire traps (12 cm × 12 cm × 25 cm), baited with peanuts (*Arachis hypogaea* Linn.). The adult animals were taken to the laboratory, while those pregnant and lactating females were released immediately *in situ* after checking. All trapped individuals were numbered, weighed, sexed, and then housed individually using PVC cages (37 cm × 26 cm × 17 cm). The animals were raised under a natural photoperiod and ambient temperature. Dry leaves and cotton were provided as nesting materials. Experimental subjects were fed for at least one week before testing, and were adequately supplied with water and feed (product of Laboratory Animal Center of Henan Province, China). The research protocol was approved by the Ethics Committee of Zhengzhou University and in accordance with guidelines outlined in the China Practice for the Care and Use of Laboratory Animals.

2.4. Germinated Acorns Cultivation

By using the flotation method [36], we selected 300 sound acorns for germinating experiment in May 2011. To reduce the influence of seed size on seedling emergence and development, the medium-size acorns of 2.5–3.5 g were chosen to conduct germination experiment. We planted acorns in a plastic box (35 cm × 25 cm × 4 cm) under the condition of natural photoperiod and ambient temperature. The acorns were covered with a layer of saw-dust, and watered timely. Status of seed germination and radicle development were examined every morning. Development of radicle was divided into two stages: (1) un-lignified radicle stage (ULRS), referring to early stage: the growing radicle was tender, white in color, and without root hair and lateral root (Figure 1c); and (2) lignified radicle stage (LRS), referring to later stage: the growing radicle has become hard, brown in color, and emerged root hair or lateral root (Figure 1d). Acorns with two types of radicles were prepared for the next experiment (Figure 1).

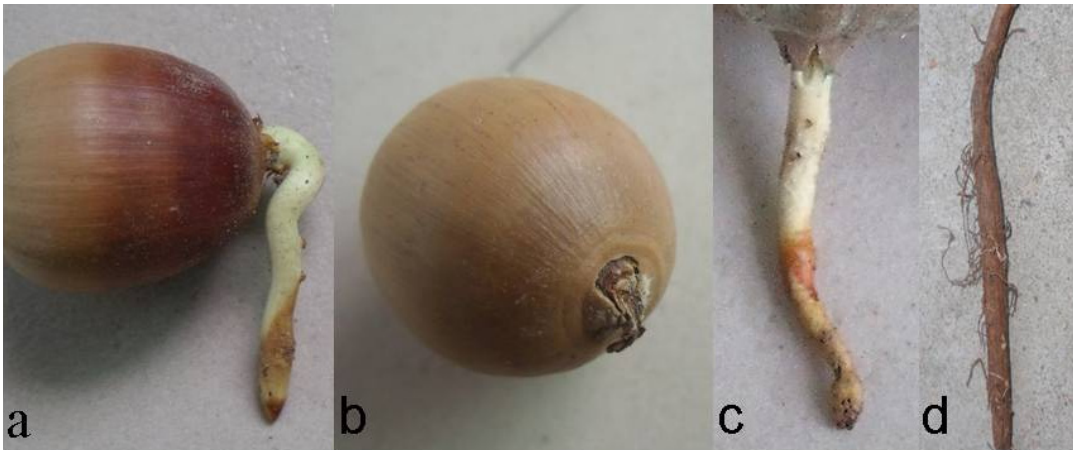

Figure 1. Development stages of radicles and radicles-excision by rodents: (**a**) germinated acorn; (**b**) the acorn with a radicle-excision by rodent; (**c**) un-lignified radicle stage (ULRS); (**d**) lignified radicle stage (LRS).

2.5. Radicle-Excision Behavior of A. Peninsulae

We conducted radicle-pruning trial in eight 4 m × 4 m semi-natural enclosures in May 2011. In a secondary forest of *Q. variabilis*, we established enclosures using 170 cm tall asbestos boards. To prevent rodent from digging and escaping, bases of asbestos boards were buried 20 cm deep in soil above brick-based ground, and the roof of each enclosure was covered with wire mesh. A nest box (40 cm × 30 cm × 20 cm) and a water bowl were placed in one corner of each enclosure, and a wooden feeder was placed in the center of each enclosure [37].

At 18:00 on the first experimental day, one *A. peninsulae* was introduced into each enclosure. Five *Q. variabilis* acorns with radicles (we chose the seeds with a radicle length >2 cm to conduct the experiment to reduce the effect of radicle length on rodents' excision behavior), marked with white plastic tag (2.5 cm × 3.5 cm, <0.3 g) [38,39], were placed in the feeder. The fate of seeds was checked and recorded at 06:00 the next day. We categorized the acorns as three types: (1) hoarded (carried into the nest or buried); (2) abandoned (removed and abandoned on the surface without consumption); (3) eaten (eaten *in situ* or after being removed). All radicle-excised acorns were collected for the next experiment. Then the rodents were taken away from enclosures, and the enclosures were cleaned, the soil was mixed again and some water was sprayed on the surface to minimize the potential cues left by former subjects. Then new nest boxes and water bowls were placed, and another eight rodents, one in each, were introduced into rearranged enclosures, and the observation and record were repeated. Thirty two rodents were used; 16 (♀/♂: 8/8) for ULRS acorn trials and 16 (♀/♂: 8/8) for LRS acorn. The experiments were conducted and finished in four successive days. Overall, 92 available radicle-excised acorns (Figure 1b), 44 of ULRS and 48 of LRS, were collected for next experiments.

2.6. Seedling Establishment from Radicle-Excised Acorns

In May 2011, 92 radicle-excised acorns (44 of ULRS and 48 of LRS) were buried (4 cm in depth) in flower pots (30 cm in height; 20 cm in diameter), one in each, filled with soil from local field and fine sand (2:1). Fifty four sound (ungerminated) acorns were assigned as control group with the same treatment as radicle-excised acorns. Then all the pots were semi-buried (the top was aboveground 1 cm) in secondary *Q. variabilis* forest and watered every three days. We checked and recorded the status and date of seedlings every three days, while measured the stem height and numbered leaves once a month. In December 2011, all the seedlings were excavated from flower pots and cleaned using fresh water. We numbered the lateral roots, measured the diameters of stalk and taproot using electronic vernier caliper (± 0.01 mm), and measured the total length of seedling with a straight scale (± 1 mm). Finally, each seedling was dried in an oven at 60 °C for 72 h and weighed with an electronic scale (± 0.01 g).

2.7. Data Analysis

All statistical analysis was carried out using SPSS for Windows (version 16.0). Two-Related Samples Wilcoxon Tests (Nonparametric Tests) were run to test the difference between the proportion of radicle-excised acorns and radicle un-excised acorns; based on our experimental purpose, we don't distinguish the difference between sexes. We compared the germination rate of sound acorns with that of radicle-excised acorns in Chi-Square Test. The dynamics of germination of perfect and radicle-excised acorns was compared in Kaplan-Meier of Survival Analysis. The seedlings, from sound acorns and radicle-excised acorns, of emergence at same day were chosen to calculate the growth rate of stalk (GRS = L/T, L-length of stem, T-time of seedling growth), and the Paired-Samples T Test was used to compare the difference of growth rate of stalk between sound acorns and radicle-excised acorns. Independent-Samples *t* Test was used to analyze the influence of radicle-excision behavior on dry biomass of seedlings (two seedlings from sound acorns were excluded because their roots were damaged by underground insects). We calculated the proportion of 0, 1, 2 and 3 lateral roots in each group (sound acorns and radicle-excised acorns) and compared the difference between groups with Chi-Square Test. All data were shown with mean ± SEM, and the significant statistical level was set at $\alpha = 0.05$.

3. Results

3.1. Radicle-Excision Behavior of A. Peninsulae

When the growing radicles were in the status of ULRS, 26.67% of acorns were eaten; 33.33% of acorns were radicle-excised and hoarded by *A. peninsulae*, but only 6.67% of acorns were hoarded with intact radicle (Figure 2a); 26.67% of germinated acorns were radicle-excised and abandoned on soil surface by rodents, while 6.67% of germinated acorns with intact radicles were abandoned on soil surface (Figure 2a).

Under the status of LRS, 25.71% of acorns were eaten; 25.72% of acorns were gnawed off radicles by rodents before hoarding, and merely 8.57% of acorns were hoarded with intact radicle (Figure 2b); 34.29% of radicle-excised acorns and 5.71% of radicle-intact acorns were abandoned on soil surface by rodents (Figure 2b).

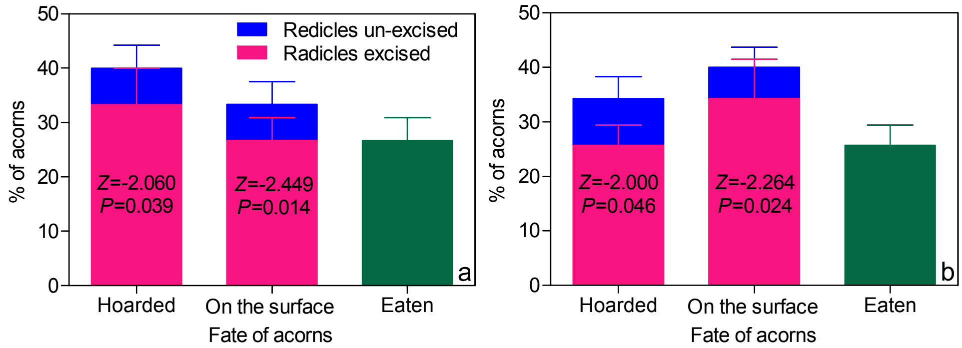

Figure 2. The processing and hoarding of rodents on germinated acorns in ULRS (**a**) and LRS (**b**). The proportion of radicle-excised acorns (pink bar) and radicle un-excised acorns (blue bar) was compared in Two-Related Samples Wilcoxon Tests.

3.2. Germination Rates in Sound and Radicle-Excised Acorns

The germination rate of sound acorns and radicle-excised acorns (in ULRS) were 79.63% (43/54) and 72.73% (32/44), and no significant difference was found between them (χ^2 = 0.320, *DF* = 1, *p* = 0.571). Surprisingly, none of the radicle-excised acorns in LRS germinated again (0/48).

3.3. Germination Dynamics in Sound and Radicle-Excised Acorns

Peak time of seedling emergence in sound acorns was from 21st to 33rd day after planting, though it was earlier than that in radicle-excised acorns (in ULRS, from 33rd to 45th day), no significant difference was found between them (Figure 3).

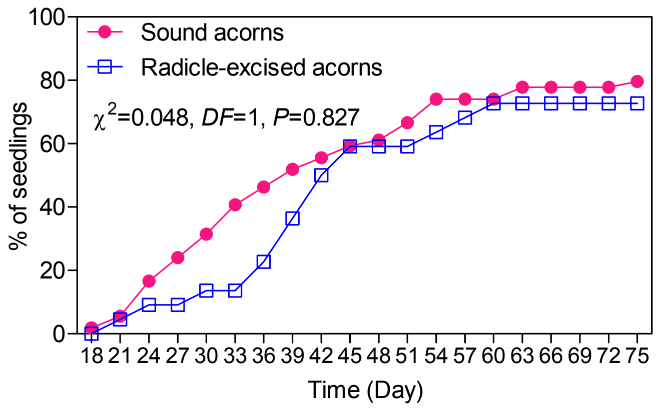

Figure 3. Seedling emerging dynamics of sound and radicle-excised acorns (ULRS).

3.4. Comparison of Parameters of Seedlings Derived from Sound and Radicle-Excised Acorns

3.4.1. Seedling Stem

The growth rates of stem from sound and radicle-excised acorns were 0.640 ± 0.029 mm/day and 0.581 ± 0.067 mm/day, but there was no significant difference found between them (Figure 4a).

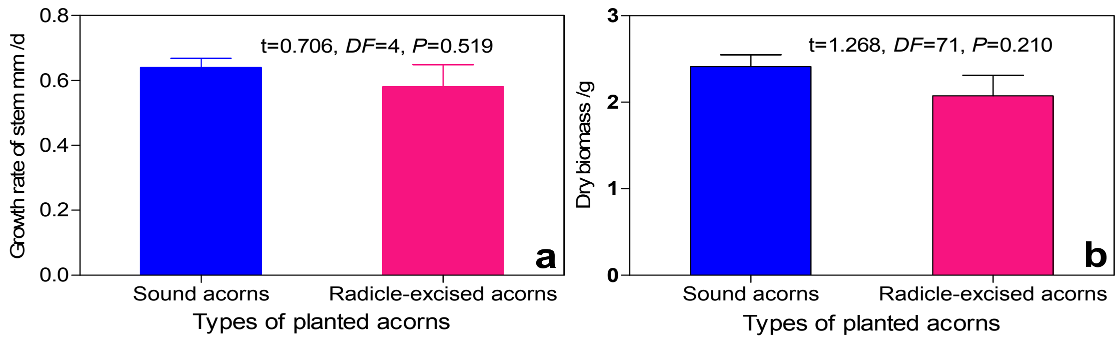

Figure 4. Growth rate of seedling stem (**a**) and dry biomass of seedlings (**b**) from sound acorns and radicle-excised acorns. To reduce the influence of emergence date (e.g., climatic factors) on seedling development, the seedlings emerging at same day were chosen to calculate the growth rate of stalk. So, the available sample was less than the total sample when compared the growth rate of stalk.

3.4.2. Seedling Biomass

The mean dry biomass of seedlings from sound acorns was 2.412 ± 0.138 g, and this value in seedlings from radicle-excised acorns was 2.074 ± 0.237 g. The difference between them was not statistically significant (Figure 4b).

3.4.3. Development of Seedling Root

Proportions of seedlings with zero (only one taproot without lateral root), one, two and three lateral roots varied obviously between two types of acorns (Table 1). In general, seedlings originated from sound acorns produced remarkable fewer lateral roots than that of radicle-excised acorns (χ^2 = 7.127, DF = 1, p = 0.008).

Table 1. Comparison on lateral roots of seedlings derived from sound and radicle-excised acorns.

Seedling Types	**Lateral Roots (Number/Percentage)**			
	Zero	**One**	**Two**	**Three**
Sound acorns	24/58.54%	11/26.83%	5/12.20%	1/2.44%
Radicle-excised acorns	10/31.25%	14/43.75%	2/6.25%	6/18.75%
p-Value	p = 0.003	p = 0.044	p = 0.157	p < 0.001

4. Discussions

4.1. Radicle-Excision Behavior of Rodents

It has been reported that several species of rodents often remove radicles before hoarding germinated seeds. Among these radicle-excising rodents, some are squirrels, e.g., *Sciurus carolinensis* Gmelin and *Tamias striatus* Linnaeus [30], *T. sibiricus* Laxmann [32]; the others are Myomorpha species with medium body size, such as *Niviventer confucianus* Milne Edwards, *Rattus flavipectus* Milne Edwards, *Maxomys surifer* Miller and *N. fulvescens* Gray [31]. In the current study, we revealed that *A. peninsulae*, a small-sized rodent species, also clearly displayed radicle-excising behavior in forests of temperate areas. We thus believed that such behavior was possibly a strategy for some species of small-sized rodents, not only squirrel and large-scale species, in managing caches.

4.2. Renewable Germination and Seedling Establishment of Radicle-Excised Acorns

Though the research on *Carapa procera* D. C. (Meliaceae) suggests that radicle-excised seeds show a lower germination rate [24], the studies on survival of radicle-excised seeds are inadequate. The results from our study provided unprecedented information for the influence of radicle-excision on re-germination of processed acorns: (1) in ULRS, radicle-excision by rodent insignificantly affected germination rate, seedling growth dynamics, stem growth rate and dry biomass of seedlings. Furthermore, radicle-excision possibly promoted differentiation and development of lateral roots; (2) in LRS, however, radicle-excision made acorns lose ability of re-germination. The difference between ULRS and LRS might be because the plumule of acorns will protrude out the epicarp once radicle lignified. So, the radicle development stage might play a key role on viability of radicle-excised acorns and seedling establishment.

4.3. Adaptive Recruitment of White Oak in Temperate Area

In temperate areas, rodents are main seed dispersers, and they scattered-hoard large quantity of acorns in fruiting season [40,41]. The burial provides suitable soil humidity for rapid germination of nondormant white oak seeds; however, some species of rodents often excise the radicles to prolong storage period once seeds sprout [18,34], which may be fatal for seedling establishment and forest recruitment. Nevertheless, our results indicating that radicle-excised acorns can re-germinate and successfully establish into seedlings provide evidence for evolutionary adaptation of plant to high seed predation, as well as enrich theories of animal-seed mutuality and forest succession.

Supplementary Materials: Figure S1. Parameters of seedling stem length and diameter, leaf length and width. Table S1. Data used for the analysis.

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Author Contributions: Yifeng Zhang, Yuhua Shi and Jiqi Lu conceived and designed the experiments and wrote the manuscript; Yifeng Zhang, Yuhua Shi and Meilin Zhu performed the experiments; Yifeng Zhang analyzed the data while Alfred M. Sichilima contributed on some linguistic technicalities and grammar.

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