Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents

Bo Wang[1,2] and Jin Chen[1,3]

[1]*CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan Province 666303, China*
[2]*Graduate School of Chinese Academy of Sciences, Beijing 100049, China*

Abstract. Scatter-hoarding rodents play an important dispersal role for many large-seeded plants. Seed traits affect their foraging behavior; however, it is difficult to isolate their effects because of the covariance among traits. Here, we used artificial seeds to partition the effects of seed size, tannin content, and nutrient content on scatter-hoarding rodents in a natural pine forest in Northwest Yunnan, China. *Apodemus*, a common genus of Old World rodents, consistently consumed small seeds in situ but removed medium-sized seeds (1.2–2.5 cm in diameter) and transported bigger seeds farther. Seed nutrient and tannin contents also significantly influenced rodents' behavior, but response varied substantially between years. Rodent behavior did involve some aspects of multivariate optimization. Our results strongly indicate that seed size is a decisive factor for scatter-hoarding rodents in the choice between seed predation and dispersal, while nutrient and tannin content played a less consistent role, possibly responding to confounding factors in the community. This result also has important implications for seed production by trees, which can improve the probability of long-distance dispersal of high-quality offspring by simply making them larger. The ability to tease apart the relative influence of different seed traits on the behavior of predators provides powerful insight into this important coevolutionary dynamic.

Key words: Apodemus; artificial seed; condensed tannin; foraging behavior; hydrolyzable tannin; nutrient content; scatter-hoarding; seed dispersal; seed predation; seed size.

INTRODUCTION

Many species of mammals, especially rodents, influence the structure and diversity of plant communities by caching plant seeds for future use but then forgetting about them (Vander Wall 1990). This unintentional dispersal of seeds by would-be predators often plays an important role in seedling regeneration, plant distribution, and plant diversity (Vander Wall 1990, 2001, Jansen et al. 2004). When scatter-hoarding rodents encounter seeds, they face two basic choices: eat them in situ or cache them for later consumption. From the plant's perspective, the second option often provides the only opportunity for long-distance dispersal of its seeds and confers many benefits (Lima et al. 1985), including the colonization of new sites and the reduction in density-dependent mortality (Jansen et al. 2004). Basic seed traits are essential factors in this coevolutionary interaction, affecting seed survival and seedling recruitment (Vander Wall 1990, Forget et al. 1998, Brewer 2001, Jansen et al. 2004, Xiao et al. 2006).

Three seed traits involved in this important plant–animal interaction are seed size, nutritional quality, and defensive secondary compounds, particularly tannic acids (Vander Wall 1990). While these traits have been the focus of substantial research, the specific effect of each trait on rodent behavior is not fully understood. For example, rodents have been shown to eat low-tannin acorns in situ and hoard high-tannin acorns (Shimada 2001*a*, Smallwood et al. 2001, Wood 2005, Xiao et al. 2008), but Xiao et al. (2006) found the opposite pattern where rodents ate in situ high-tannin seeds (i.e., *Quercus serrata* and *Cyclobalanopsis glauca*) and transported low-tannin seeds (i.e., *Lithocarpus harlandii* and *Camellia oleifera*).

Large seeds are often removed by rodents more than small seeds (Moles et al. 2003), indicating that seed size may play a central role in seed fate (Vander Wall 1995, 2003, Forget et al. 1998, Xiao et al. 2005, 2006). While larger seeds generally contain more energy, different plant species do vary in the relationship between seed size and other traits (Blate et al. 1998); therefore it is not clear whether seed predators are responding simply to seed size or whether their behavior has been shaped through a long coevolutionary process with their sympatric plants (Xiao et al. 2006). More generally, teasing apart the relative effects of multiple traits on seed-caching behavior is difficult in studies that use different species of natural seeds because seed traits are correlated in different ways, depending on the plant species.

[3] Corresponding author. E-mail address: cj@xtbg.org.cn

Some previous studies have properly controlled for the association of traits and how they affect rodent caching behavior. To understand how seed perishability affected squirrel caching behavior, Hadj-Chikh et al. (1996) examined the effect of seed perishability on squirrel caching behavior by using seeds from a single species, which only varied in their perishability. Jansen et al. (2004) used *Carapa procera*, a large-seeded rain forest tree, to investigate how seed mass influences seed dispersal and predation. *Carapa procera* seeds naturally vary over a 20-fold range in seed mass, allowing control for plant species across a wide range of seed sizes (Jansen et al. 2004). However, this kind of research still suffers from the limitation of trait covariation, such as the association of seed size and energy content per seed.

Using artificial foodstuffs provides the opportunity to test animal behavioral responses to specific traits by varying single traits experimentally, while keeping other traits constant (Smallwood and Peters 1986, Lewis et al. 2001, Downs et al. 2003, Bergvall and Leimar 2005). For example, Smallwood and Peters (1986) used acorn flour with additional fat and tannin to observe food preferences by squirrels and suggested additional fat might help to attenuate the effects of tannin. Steele et al. (2001) used artificial acorns (red oak acorn shells with ground cotyledon of white oak acorns, and vice versa) in order to determine which cue (visual vs. olfactory) rodents used for seed caching. Here, we developed a series of experiments using artificial seeds to isolate the effects of seed size, nutrient and tannin content on rodent caching behavior and seed dispersal distance. With a careful design of the artificial seeds, we tested the following predictions: (1) rodents would exhibit a significant and consistent response to each independently tested trait and (2) the seeds with the best combination of traits should have the highest removal rate or greatest dispersal distance.

METHODS

Study site

This study was carried out during September to November in 2006 and 2007 in a pine forest in the Shangri-La Alpine Botanical Garden, Hengduan Mountains, Yunnan province, southwestern China (27°54′ N, 99°38′ E, altitude 3456 m). The annual mean temperature is ~5.4°C, and annual rainfall is 625 mm, much of which occurs from May to October (Zhang et al. 2006). The forest is mostly natural with little human disturbance. *Pinus densata* is the dominant tree species, which coexists with several other tree species, including *Pinus armandi*, *Betula delavayi*, *Picea brachytyla*, and *Populus* spp. The understory is dominated by the shrubs *Quercus monimotricha* and some *Rhododendron* spp. The ground flora is poorly developed, consisting of only a few herbs and mosses. The forest in the botanical garden borders the natural forest; thus, the rodent community in the study site was not isolated from the natural forest. Two small kinds of nocturnal rodents, *Apodemus latronum*

and *A. chevrieri*, were the most abundant seed predators in the forest. The densities of the two *Apodemus* species were very similar between years (average trap success was 5.3% and 5.6% in 2006 and 2007, respectively), according to our trapping census.

Nutrient and tannin contents of natural seeds and artificial seed preparation

In order to determine the variation in nutrient and tannin contents of seeds, we collected 11 species of seeds in the forest for analysis. The mean caloric content of the 11 species was 10.29 ± 1.30 kJ/g (mean ± SE), with a range of 2.37–18.80 kJ/g. Tannin content was 7.77% ± 2.88%, with a range of 0–26.48%. These data were used as a guideline for the nutrient and tannin contents in our artificial seeds.

We used clay, peanut powder, and tannin to produce artificial seeds. Both the clay and the peanut powder were dried in the sun and ground in a mortar until it passed through a 1-mm screen. The clay power was mixed with different proportions of peanut powder and tannin powder and thoroughly homogenized, and water was added to bring each batch to a doughy consistency. The batches were then formed into the shape of a ball by hand and left to dry naturally. This clay is soft when wet but becomes hard when dry. Hands were treated with peanut powder in order to exclude any olfactory interference while preparing the seeds. The clay was collected from ~60 cm depth in the lateritic red soil in humid tropical southwestern Yunnan. The peanuts were bought from a local market. We used two types of tannins in this study: hydrolyzable tannin and condensed tannin. The former was tannic acid ($C_{76}H_{52}O_{46}$, molecular mass 1701.23; Reijinte Chemistry, Tianjin, China), and the latter was a vegetable extract from barks of waxberry trees (*Myrica* sp.) (tannin content 68%, Guangshengxiang Phytochemistry Factory, Yunnan, China). We used *Myrica* tannins because they were standardized and commercially available.

A 15-cm thin steel thread with a small red plastic tag (2.5 cm in length and 0.7 cm in width) was connected to each artificial seed. Each tag was numbered for seed identification. When rodents buried the seeds in the soil, the tags were usually left on the surface, making the seeds easy to relocate. Six plots (2 × 2 m) >50 m apart from each other were set up. At each plot, we located nine seed release points in a 3 × 3 grid, with ~1 m between points. Each circle-shaped point was ~15 cm in diameter, and the seeds were placed along the circle with the tags located outward.

Experiment 1: seeds with different tannin content

Seeds were ~15 mm in diameter, consisting of 50% peanut powder (total caloric content 13.34 kJ/g) and 50% clay with variable contents of tannins. The most important phenolic compounds in plants are hydrolyzable and condensed tannins. Both hydrolyzable tannins (Smallwood and Peters 1986, Skopec et al. 2004,

Bergvall et al. 2006) and condensed tannins (Downs et al. 2003) have been reported to discourage consumption by rodents or other mammals. In this study, we tested the effect of hydrolyzable and condensed tannins on caching behavior. By adding different amounts of tannins, we created tannin contents of 0.1%, 0.5%, 1%, 5%, 10%, 15%, and 25% for both hydrolyzable and condensed tannins, respectively. Thus, we had 15 treatments including one control with 0% tannin content. In 2006 and 2007, 30 labeled seeds (two seeds × 15 treatments) were randomly placed into each seed release point resulting in a total of 270 artificial seeds per plot (each plot contained nine seed release points). Each seed treatment was represented by 108 seeds spread evenly over the six plots (18 seeds per plot). A total of 1620 seeds were placed per year.

Experiment 2: seeds with different sizes

Using seeds consisting of 50% peanut powder and 50% clay (total caloric content 13.34 kJ/g), we set up 10 seed-size treatments using seeds with different diameters: 0.2, 0.4, 0.6, 0.9, 1.2, 1.5, 2.0, 2.5, 3.0, and 4.0 cm. In 2007, 20 labeled seeds (two seeds × 10 treatments) were randomly placed into each seed release point resulting in a total of 180 artificial seeds per plot. Each seed treatment was represented by 108 seeds spread evenly over the six plots (18 seeds per plot). A total of 1080 seeds were placed.

Experiment 3: seeds with different nutrient content

For this experiment, we used seeds with 15 mm diameter with varying ratios of clay and peanut powder content. We used eight seed nutrient content treatments, with the following percentage of peanut powder: 0%, 10%, 20%, 30%, 40%, 50%, 60%, and 70%. Thus the caloric contents of these seeds were 0, 2.67, 5.33, 8.00, 10.67, 13.34, 16.00, and 18.67 kJ/g, respectively. The control seeds were made of clay, using water containing the odor of peanut powder so that the seeds smelled like peanuts without containing peanut powder. Water added for preparing the control seeds was soaked by peanut powder in advance. Therefore the seeds contained no nutritional value or tannins. In 2007, 16 labeled seeds (two seeds × eight treatments) were placed into each seed release point resulting in a total of 144 artificial seeds per plot. Each seed treatment thus consisted of 108 seeds spread evenly over the six plots (18 seeds per plot). A total of 864 seeds were placed.

Experiment 4: seeds with combined traits

We devised 15 seed treatments with varying levels of seed size, peanut powder, clay, and tannin acid content. We used three seed sizes: big (2.0 cm in diameter), medium (1.0 cm in diameter), and small (0.5 cm in diameter); two nutrition levels: high (65.2% peanut powder, 17.39 kJ/g), and low (32.6% peanut powder, 8.69 kJ/g); and two tannin concentration levels: with tannins (10% in mass) and without tannins. Thus we had

12 kinds ($3 \times 2 \times 2 = 12$) of artificial seeds with different combinations of seed traits. To this we added three control seed treatments (big, medium, and small) using seeds that had the odor of peanuts but contained no nutritional value or tannins. Sixteen plots were established in 2006 and 2007, with the plots at least 30 m apart. At each plot, we placed 60 tagged seeds (four seeds × 15 treatments) in a 6×10 grid, respectively, with ~15 cm between seeds. A total of 960 seeds representing the 15 treatments were placed per year.

Seed retrieval

After the seeds were placed, we checked the tagged seeds at each seed source to record seeds harvested by rodents. We searched the ground around each seed-placement plot after days 1, 2, 3, 4, 6, 8, 12, 16, 20, 28, and 36. We conducted a complete search within 20 m of each plot in all directions to relocate the removed seeds. We also conducted an extra search in a larger area in order to relocate as many of the seeds as possible. When we found a cache, we carefully retrieved the seeds and recorded their exact location with a directional angle and the distance to their original seed sources.

Seed fates were grouped into two categories: (1) eaten in situ, leaving only plastic tags and seed fragments on the ground surface of the original release plot; and (2) removed, including: cached (buried intact in the soil or deposited intact on the soil surface), eaten after being transported (removed by the rodents from the original release plots before being eaten), and missing (seeds that were not found within the search area, hence with an unknown fate).

Statistical analysis

Linear regression models were used to determine relationships between seed fates and tannin and nutrient contents, and also the dispersal distances and the three seed traits. Quadratic curve estimation was used to examine the relationship between seed size and the number of seeds with different seed fates. A chi-square test was used to examine the different proportions of seed fates among seeds with different size, tannin and nutrient content. Three-way ANOVA was used to examine the effects of seed size, tannin, and nutrient on the proportion of different seed fates and distance of cached seeds in experiment 4. All analyses were conducted using the software SPSS 11.5 (SPSS 2002).

RESULTS

Effects of tannin type and content on seed fate

Seed predator behavior is highly variable between years in response to tannin content. In 2006, there was a significantly positive relationship between tannin content and the percentage of seeds removed for both tannin types, while the distance of cached seeds was not significantly correlated with tannin content (Figs. 1a–d and 2a, b). In 2007, however, tannin content for both hydrolyzable and condensed tannins was not signifi-
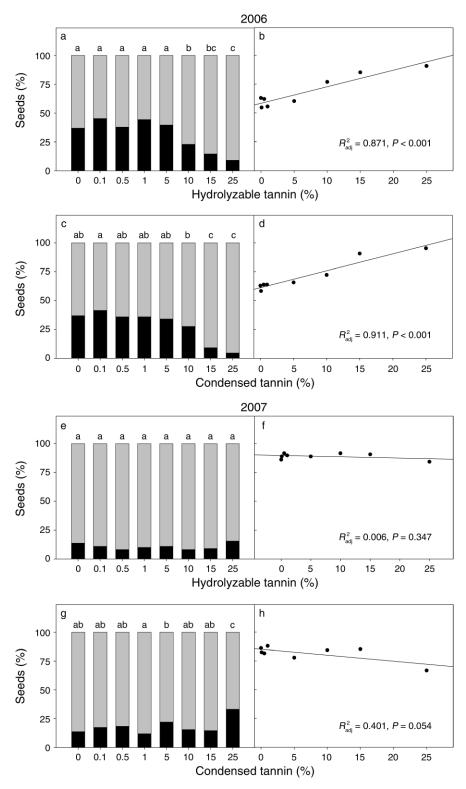
2006

FIG. 1. Differences in seed fates among seeds with different tannin contents and the relationship between number of seeds removed and tannin contents in (a–d) 2006 and (e–h) 2007 in a pine forest, southwestern China (108 seeds·[tannin type]$^{-1}$·[tannin content]$^{-1}$). Black bars represent seeds eaten in situ, while gray bars and solid circles represent seeds removed. Of the 1620 seeds used each year, no seeds remained intact in situ. A chi-square test was used to test the significance of differences between tannin contents. Different letters indicate significant differences among seed treatments ($P < 0.05$). Linear regression models were used to test the significance of the relationships between the percentage of seeds dispersed and tannin contents. Panels (a), (c), (e), and (g) show the percentage of seeds with different fates among different tannin types: (a) hydrolyzable tannin content treatments in 2006, (c)
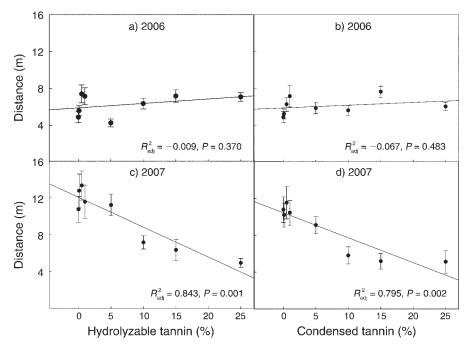
FIG. 2. Relationship between dispersal distance (mean ± SE) of cached seeds and seed tannin content in experiment 1. Linear regression models were used to test for significance of the relationships. (a) Hydrolyzable tannin seeds ($n = 489$) cached in 2006. Sample size for each category (from 0% to 25%) was 50, 47, 53, 41, 57, 73, 83, and 85, respectively. (b) Condensed tannin seeds ($n = 464$) cached in 2006. Sample size for each category was 50, 45, 51, 47, 54, 64, 72, and 81, respectively. (c) Hydrolyzable tannin seeds ($n = 353$) cached in 2007. Sample size for each category was 29, 27, 38, 37, 43, 54, 61, and 64, respectively. (d) Condensed tannin seeds ($n = 314$) cached in 2007. Sample size for each category was 29, 34, 31, 40, 43, 52, 61, and 24, respectively.

cantly correlated with the percentage of seeds removed (Fig. 1e–h), while significant negative relationships were observed between tannin content and the distance of cached seeds for hydrolyzable and condensed tannins (Fig. 2c, d).

Of the 1620 artificial seeds used in this experiment, 31 and 258 of the removed seeds were eaten after being dispersed in 2006 and 2007, respectively. A significant negative relationship between tannin content and transported distance of the seeds eaten after being transported for both hydrolyzable tannin ($R^2_{adj} = 0.702$, $P = 0.006$) and condensed tannin ($R^2_{adj} = 0.646$, $P = 0.010$) was recorded in 2007 but not in 2006 ($P > 0.05$).

Effects of seed size on seed fate

Seeds with different sizes showed significant differences in seed removal rates ($\chi^2 = 462.270$, df = 9, $P < 0.001$; Fig. 3a). A nonsignificant linear regression was found between seed size and seed fate; however, there was a significant unimodal relationship between seed size and the percentage of seeds removed ($R^2_{adj} = 0.757$, P

$= 0.003$, using quadratic curve estimation; Fig. 3b). Medium-sized seeds with a diameter of 1.2–2.5 cm were removed more frequently than other seeds (Fig. 3a, b).

Of the 355 seeds cached, there was a significant positive relationship between cached distance and seed size ($R^2_{adj} = 0.971$, $P < 0.001$; Fig. 3c). A total of 144 seeds were eaten after being transported, and the relationship between removal distance of these seeds and seed size was also significantly positive ($R^2_{adj} = 0.677$, $P = 0.002$; Fig. 3d).

Effects of seed nutrient content on seed fates

Of the 864 seeds used in experiment 3, only two seeds were consumed in situ. Among the 340 cached seeds in eight nutrient contents, a significant positive relationship was found between dispersal distance and nutrient content in 2007 ($R^2_{adj} = 0.746$, $P = 0.004$; Fig. 4).

Only 23 seeds were found eaten after being removed, and there was no significant relationship between transported distance and nutrient content ($P > 0.05$).

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condensed tannin content treatments in 2006, (e) hydrolyzable tannin content treatments in 2007, and (g) condensed tannin content treatments in 2007. Panels (b), (d), (f), and (h) show the relationship between different tannin types and the percentage of removed seeds in two years: (b) hydrolyzable tannin contents in 2006, (d) condensed tannin contents in 2006, (f) hydrolyzable tannin contents in 2007, and (h) condensed tannin contents in 2007.
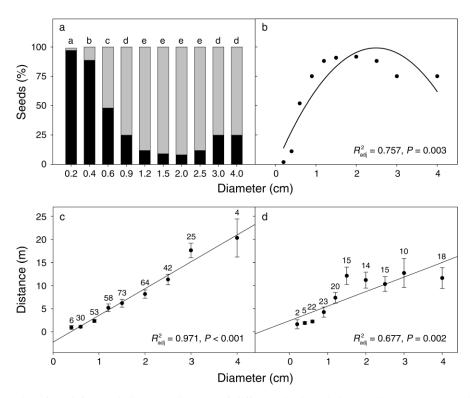
FIG. 3. Results of seed fate and dispersal distance of different-sized seeds in experiment 2 (108 seeds tannin per treatment). (a) Differences of seed fates among different-sized seeds. Black bars stand for seeds eaten in situ, and gray bars stand for seeds removed. A chi-square test was used to test significance of the differences. Different letters indicate significant differences among different seed size classes ($P < 0.05$). (b) Relationship between numbers of seeds removed and seed size in experiment 2. Quadratic curve estimation was used to test the significance of the relationship. (c) Relationship between the dispersal distance of cached seeds (mean ± SE) and seed size. (d) Relationship between the dispersal distance of seeds that were eaten after being dispersed (mean ± SE) and seed size. Numbers above the bars are the sample sizes.

Seed fates of the combined treatment experiment

Across both years, seed size was a strong predictor for seed removal (2006, $F_{2,2} = 986.52$, $P < 0.001$; 2007, $F_{2,2} = 131.47$, $P < 0.001$); large seeds were removed more often than medium- and small-sized ones, while they were less often eaten in situ in both years (Fig. 5). Tannin and nutrient content were not significant in predicting seed fates except tannin content in 2006, where high tannin content was associated with high seed removal ($F_{1,2} = 29.16$, $P < 0.05$). Interactions for all covariates were tested, and all were not significant except in 2006, where size and nutrition showed a significant interaction ($F_{2,2} = 29.08$, $P < 0.05$). High nutrient content was associated with higher seed removal in both medium-sized and big seeds than in the same-sized seeds with low nutrition content treatment (Fig. 5).

Seed size was also a strong predictor of the distance that both cached seeds (2006, $F_{2,141} = 11.92$, $P < 0.001$; 2007, $F_{2,145} = 14.26$, $P < 0.001$) and eaten seeds (2006, $F_{2,140} = 11.23$, $P < 0.001$; 2007, $F_{2,83} = 12.45$, $P < 0.001$) were transported: seeds that were larger were transported farther. Tannin and nutrient content were not

significant in either year (Fig. 6). Interactions for all covariates were tested, and all were not significant in predicting the distance for cached seeds and eaten seeds after being transported.
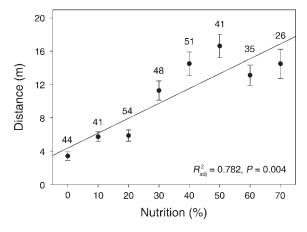

FIG. 4. Relationship between the dispersal distance of cached seeds (mean ± SE) and seed nutrient content. Linear regression was used to test the significance of the relationships. Numbers above the bars are the sample sizes.
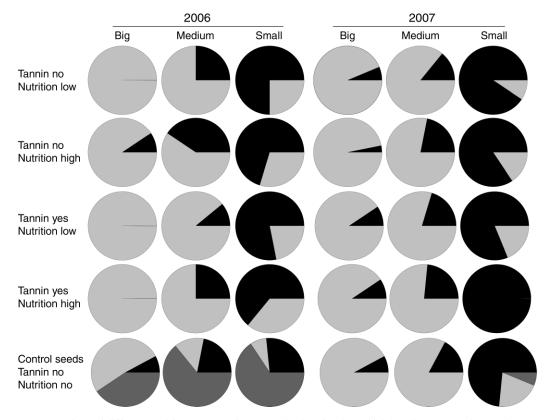
FIG. 5. Proportions of different seed fates (removed vs. eaten in situ) for the artificial seed treatments in experiment 4. Light gray parts represent seeds removed, black parts represent seeds eaten in situ, and dark gray parts represent seeds left intact in situ. Data were pooled (64 seeds per treatment) for the 16 plots. Seed size had a significant effect on seed fate in both years ($P < 0.01$). Large seeds were removed more often than medium and small ones and were less often eaten in situ. Tannin content had a significant but small effect on seed fate in 2006 ($P < 0.05$) but not in 2007 ($P > 0.05$). Seeds containing tannin were removed more than seeds with no tannin but were eaten less in situ in 2006. Nutrient content had no effect on seed fate in either year ($P > 0.05$).

DISCUSSION

In this study, rodent caching behavior responded to the three traits tested by the univariate experiments: seed size, tannin and nutrient content. Rodent behavior does involve some aspect of multivariate optimization, which differed between years. However, seed size demonstrated a consistent and overwhelming effect in predicting seed fate, as well as the distance of dispersal for cached seeds in the multivariate experiment. Tannin content was also a significant predictor of seed fate but the strength and the direction of this relationship were not consistent between years.

Our results indicate that scatter-hoarding rodents choose which seeds to cache primarily based on an "ideal" seed size (Fig. 3), and larger seeds were more likely to be dispersed farther. Rodents even preferentially removed big seeds that had no nutritional value, strongly illustrating the influence of seed size as a "proxy" for other traits (Fig. 5). Similar results were found by Jansen et al. (2004), where larger seeds of a single tree species, with a wide range of seed sizes, were removed faster, were more likely to be scatter-hoarded, and were dispersed farther away than smaller ones.

Moore et al. (2007) investigated five seed types at 15 locations and three forested sites in Pennsylvania, USA and 29 forest fragments in Indiana, USA, across five different years. Seeds with greater energy content were consistently moved farther than less profitable food items, which suggests, seed size, because of its generally positive correlation with energy content, played a significant role in influencing rodents' caching behavior. Rodents have exhibited significant preference for larger seeds in many other studies (Vander Wall 1995, 2003, Forget et al. 1998, Xiao et al. 2004, 2006, but see Blate et al. 1998, Theimer 2003).

Several non-mutually exclusive explanations exist in the literature for this behavior. Large seeds often contain high nutritional value (Vander Wall 1995, 2003, Forget et al. 1998, Xiao et al. 2006); even if these seeds germinate, they can retain their value longer than small seeds (Jansen et al. 2002). Additionally, by choosing large seeds, rodents need to keep track of fewer caches to obtain the same absolute value (Jansen et al. 2002).

Handling time for larger seeds could also be a major factor, as the rodents in this study are relatively small and the increased handling time exposes them to greater
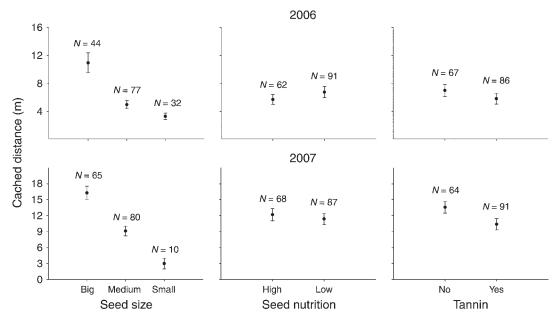
FIG. 6. Comparisons of the dispersal distance (cached seeds) of different artificial seed treatments in experiment 4. Data were pooled (64 seeds per treatment) for the 16 plots. Distances (mean ± SE) of dispersed seeds were significantly different among different-sized seeds both in 2006 and 2007 ($P < 0.001$). Seed nutrient and tannin content had no significant effects on distance of cached seeds in either year ($P > 0.05$).

predation risk (Lima 1985). Additionally, the rodents did not prefer the largest seeds but instead preferentially dispersed intermediate-sized seeds (1.2–2.5 cm in diameter), suggesting that simple body size of the seed predator can limit the attractiveness of large seeds.

When seed size is controlled, nutrient content also played a significant role in the choice of seeds removed and dispersal distance indicating that rodents did have the ability to determine seed nutrient content. A number of studies have found similar results (Hurly and Robertson 1987, Moreno and Carrascal 1995, Jansen and Forget 2001, Jansen et al. 2004, Xiao et al. 2006, Moore et al. 2007).

The relationship between seed tannin content and rodent caching behavior appears to be complex, as a significant effect was observed but it differed in strength and direction between years (Figs. 1 and 2). Some studies suggested that rodents prefer to cache acorns with a high tannin level and consume those with a low tannin level (Shimada 2001a, Smallwood et al. 2001, Wood 2005, Xiao et al. 2008, but see Xiao et al. 2006). Several hypotheses have been brought forward to explain this phenomenon: (1) tannins in cached seeds may be reduced through time either by abiotic environmental factors or physiological processes in the seeds (but see Dixon et al. 1997, Shimada 2001b, Smallwood et al. 2001); (2) seeds with high tannin content may be less perishable and suffer less cotyledon loss to insects (Weckerly et al. 1989, Smallwood et al. 2001); and, (3) high tannin content may be correlated with delayed germination times and rodents may be choosing these seeds because of their longer storage

times and not because of the amount of tannin (Smallwood et al. 2001, Steele et al. 2001).

We obtained conflicting results between years, with high tannin seeds preferentially cached in 2006 while seeds with higher tannin contents were transported nearer than seeds with lower tannin contents in 2007. These results indicate the rodent caching behavior in response to tannin content is probably a multivariate response to several factors external to this study. While rodent population fluctuation and seed : rodent abundances may play a role in some situations (Vander Wall 2001, DeMattia et al. 2004, Jansen et al. 2004, Li and Zhang 2007, Moore et al. 2007), rodent densities in our study between the two years were very similar (average trap success: 5.3% vs. 5.6%) and *A. latronum* and *A. chevrieri* were the dominant species in both years. Significantly more seeds were removed in 2007 (85.2% ± 1.7%) than in 2006 (70.6% ± 3.6%) (paired *t* test, $t =$ 3.241, $P = 0.006$) and the seeds were removed faster in 2007 (after only six days compared to 16 days in 2006), suggesting differences in seed availability at the community level; however no substantial differences in overall seed production were apparent to casual field observation. Although we have no data on relative abundances of natural seed availability, given the variation in tannin content among the tree species present on our study area (Wang and Chen 2008), some species (e.g., *Iris bulleyana* [26.5%] and *Abies* sp. [25.7%]) were very high in tannin content while other species were very low (e.g., *Hemsleya pedunculosum*, 0%; *Pinus armandii*, 1.0%; *Pinus densata*, 0.8%) (Wang and Chen 2008). Differences in seed production among these trees

could have altered the background level of tannin concentrations in seeds and thereby altered rodent responses to our artificial seeds. Nonetheless, this study suggests that rodents' responses to seed tannins are not consistent. Therefore, the selection upon tannin in seeds by rodent dispersal may not be very significant.

Seed sizes of different plants are the consequence of evolutionary trade-offs; seed production, seed predation, and seedling dynamics may all affect seed size evolution (Howe 1989, Blate et al. 1998). Seed size was shown to be an overwhelming and consistent indicator of whether and how far seeds were dispersed in this study. Thus rodent community composition may affect plant evolution and demography. Changes in rodent body size within species and the rodents' community composition will therefore potentially influence seed size preference and the long-term seed size evolution in the community.

The relationship between seed size and many other important traits, including nutrient composition, secondary compounds, digestibility, taste, and odor, is often complex and nonlinear (Blate et al. 1998, Kollmann et al. 1998, Shimada 2001b, Xiao et al. 2005, 2006), possibly affected by coevolutionary dynamics. Our study isolated the effects for three main variables by using artificial seeds, illustrating the importance of seed size alone as a "proxy trait," which is normally highly correlated with other important seed traits. Compared to most research using different-sized seed of the same species (but see Jansen et al. 2004), this study overcomes the disadvantage that the range of intraspecific seed size is often very limited (also see discussion in Jansen et al. 2004).

CONCLUSION

In this study, we effectively used artificial seeds to experimentally tease apart the effect of seed size, tannin and nutrient content on rodent seed-caching behavior. All three seed traits were important to rodent foraging behavior; however, seed size proved to be an overwhelming and consistent indicator of whether and how far seeds were dispersed. This seed size effect was true despite the fact that overall harvest time and rate differed between years and tannin content actually had a conflicting effect each year. Our approach could be adapted in future studies to gain a better understanding of the coevolutionary dynamics of plant seed production and seed predators. The complex selection pressure imposed by scatter-hoarding rodents on seed-producing plants, primarily long-lived woody trees, is poorly understood and requires further and more detailed study.

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