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Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China

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Abstract

Based on the complex seed packaging strategies involving morphology, nutrition quality and secondary chemistry, spatial and temporal variation of seed predation and removal by granivorous rodents was examined among six sympatric large-seeded tree species with different seed traits: *Lithocarpus harlandii*, *Quercus variabilis*, *Q. serrata*, *Cyclobalanopsis glauca* and *Castanopsis fargesii* (Fagaceae); *Camellia oleifera* (Theaceae) across different stands and seasons in a subtropical evergreen broadleaved forest, Southwest China. The smallest seeds of *Castanopsis fargesii* with lower tannin concentration, *L. harlandii* with the largest seed size and *Camellia oleifera* with high fat concentration, were harvested more quickly than the apparently less preferred seeds of *Q. variabilis*, *Q. serrata* and *C. glauca* with higher tannin concentration. Larger (*L. harlandii* and *Q. variabilis*) or high fat seeds (*Camellia oleifera*) have higher levels of removal and lower levels of instant consumption than smaller seeds (*Castanopsis fargesii*, *Q. serrata* and *C. glauca*) for both stand and season. Results showed that high fat or large seeds are harvested more quickly than small or medium seeds with high tannin concentration, and that high fat or large seeds are also more likely to be removed than small or medium seeds with high tannin concentration. Moreover, seed predation and removal are consistent among stands and seasons. Innate seed traits are shown to be important in determining whether a given seed is eaten or removed when rodents are provided uniform number of seeds with differing traits. The hierarchical preference for larger or high fat seeds is maintained when background seed abundance varies in time and space.
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Keywords: Seed preference; Seed size; Nutritional quality; Tannin; Granivorous rodents

1. Introduction

The radiation and present diversity of many angiosperms is recognized as being concurrent with a transition from small-seeded wind-dispersed species to large-seeded animal-dispersed species (Vander Wall, 2001). Animal-dispersed seeds possess traits that, in addition to affecting germination, growth and development, also influence seed predation, removal and dispersal by animals. Seed predation, removal and scatter-hoarding by granivorous rodents have a considerable impact on seedling regeneration, plant distribution and plant diversity (Price and Jenkins, 1986; Brown and Heske, 1990; Vander Wall, 1990, 2001; Hulme, 1998, 2002; Howe

and Brown, 2001; Jansen and Forget, 2001). Generally, seed predation and removal by granivorous rodents have different consequences for plant reproductive success, since seed predation often refers to seed mortality through consumption while seed removal at least partly links to successful seed dispersal through scatter-hoarding. Therefore, it is necessary to compare the relative importance of predation in situ and removal by granivorous rodents. In addition, the role of granivorous rodents in plant demography is still controversial. In many ecosystems, granivorous rodents are mainly seed predators (see reviews in Hulme, 1998, 2002), but still some seeds might survive to establish a seedling after removal (e.g. Abbott and Quink, 1970; Forget and Milleron, 1991; Vander Wall, 1993, 1994; Zhang and Wang, 2001; Li and Zhang, 2003; Xiao et al., 2004a).

Innate seed traits like size, nutritional quality, and morphological and chemical defenses, can influence seed

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predation, removal and caching by granivorous rodents; this in turn affects seed survival and seedling recruitment (e.g. Price and Jenkins, 1986; Vander Wall, 1990; Forget et al., 1998; Brewer, 2001; Jansen and Forget, 2001; Chauvet et al., 2004). However, the relationship between innate seed traits and seed fate (seed predation, removal, caching and survival) still remains unresolved. In general, large seeds are expected to have higher seed predation and lower survivorship than small seeds (see Moles et al., 2003, and references therein). However, recent studies on seed dispersal by granivorous rodents have shown that large seeds are more likely to be removed and then cached, rather than eaten in situ (e.g. Vander Wall, 1995, 2003; Forget et al., 1998). Granivorous rodents often prefer to remove and cache larger seeds or seeds with higher fat content (Smith and Reichman, 1984; Jansen and Forget, 2001; Xiao et al., 2003a). Increased handling time can increase the predation risk for granivorous rodents. Seeds with a harder seed hull had higher rates of seed removal and reduced instant consumption compared to seeds with softer hulls (Jacobs, 1992; Hadj-Chikh et al., 1996; Xiao et al., 2003a; Zhang et al., 2004).

Kollmann et al. (1998) observed that rodent seed predation rates are consistent among sites, seasons and years based on time-to-disappearance, i.e. the time that a given seed is eaten or removed by animals after seed exposure. Time-to-disappearance, however, does not differentiate between seed predation and removal. Further, the consistency in seed predation or removal suggests that innate seed traits are primary factors in determining seed preferences by seed-eating animals. In addition, time-to-disappearance may be greatly affected by seed abundance at the population and/or community level (e.g. Hoshizaki and Humle, 2002; Chauvet et al., 2004). Moreover, variation of seed abundance could also largely affect seed predation, seed removal and caching (e.g. Forget and Milleron, 1991; Forget, 1992; Hulme and Hunt, 1999; Xiao et al., 2005). For example, the less-preferred species might experience reduced seed predation when the seed abundance of other more preferred species increases (Hoshizaki and Humle, 2002). These findings suggest a behavioral dichotomy (consumption or caching) in initial seed utilization by small rodents that is complexly affected by seed abundance, size, energy, hardness and defensive chemistry (e.g. Shimada, 2001; Jansen et al., 2002).

We examined spatial and temporal variation of seed predation and removal by granivorous rodents among six sympatric large-seeded tree species that differ in size and other traits (e.g. fat and tannin concentration) in a subtropical evergreen broadleaved forest, Southwest China across different stands and seasons. Our preliminary observations suggested that granivorous rodents (e.g. Edward's long-tailed rats, Leopoldamys edwardsi) were very important in natural regeneration of these large-seeded species (Xiao et al., 2001, 2003a, 2004a,b; Zhang et al., 2004). Thus, we developed the following testable hypotheses to examine seed predation and seed removal at the cafeteria plots:

(I) Large or high-value (e.g. high fat concentration or low tannin concentration) seeds are harvested more quickly than small or low-value seeds with high tannin concentration.

(II) Large or high-value seeds are more likely to be removed, rather than eaten in situ, compared with low-value seeds. We predicted that seed mass is positively correlated with seed removal, but negatively with seed eaten in situ.

(III) Since innate seed traits are more likely to determine seed predation and removal for given seeds according to the former hypotheses: seed predation and removal should be consistent among stands and seasons (based on the time-to-harvest = time-to-disappearance in Kollmann et al., 1998), and in the ratios of seeds eaten versus those removed within and among species. We further hypothesize that these rates and ratios are related to the complex seed packaging strategies involving morphology, nutrition and secondary chemistry operating in the system.

2. Study site

The study was conducted from October to December 2000 in the Banruosi Experimental Forest (area, over 100 ha; elevation 700–1000 m, $31°4'$N, $103°43'$E) in Dujiangyan City, Sichuan Province, Southwest China. The site lies in the middle of the subtropical zone, with a mean annual temperature of $15.2\,°C$, and an annual precipitation of 1200–1800 mm (Chen, 2000). The weather is often cloudy and foggy, with annual hours of sunlight typically in the range 800–1000 and a mean annual relative humidity of more than 80%.

Subtropical evergreen broadleaved forest (elevation, 700–1500 m) in the Dujiangyan Region of Sichuan Province, China are a mosaic often isolated and fragmented by agricultural development resulting in populations of many otherwise common tree species being very rare or even extinct due to deforestation (Chen, 2000). The experimental forest chosen for this study is mainly dependant on natural seed regeneration of native tree species though modern human interference (e.g. logging and agricultural development) has greatly influenced its seed regeneration. The variation in stand age and vegetation structure provided a natural division into three stand types: primary stands (>80–90 years), secondary stands (<50 years) and shrublands (<10 years; Table 1). In these stands, dominant or commom tree species included Castanopsis fargesii, Quercus variabilis, Pinus massoniana, Acer catalpifolium, Q. serrata, Lithocarpus harlandii, Phoebe zhenman, Cyclobalanopsis glauca, and Camellia oleifera, but their populations varied greatly (Zhishu Xiao, personal observation). Besides the above stands, parts of secondary stands and shrublands had been reforested by planting Cryptomeria fortunei in 1996. At the time of the study, these reforested plantations resembled the shrublands (Table 1).

In late October 2000, seven rodent species were trapped over 150 trap nights across the four stand types: white-bellied rats (Niviventer confucianus), chestnut rats (N. fulvescens), Himalayan rats (Rattus nitidus), Edward's long-tailed rats (Leopoldamys edwardsi), Bower's rats (Berylmys bowersi), Sichuan field mice (Apodemus latronum) and Chevrier's field mice (A. chevrieri) (Xiao et al., 2002). Total trap success of

Table 1
Tree abundance and seed availability of the large-seeded species used in this study

Study species	Primary stand		Secondary stand		Shrubland		Plantation	
	Tree abundance[a]	Seed availability[b]	Tree abundance[a]	Seed availability[b]	Tree abundance[a]	Seed availability[b]	Tree abundance[a]	Seed availability[b]
Quercus variabilis	**	++	***	+++	*	–	*	–
Q. serrata	*	+	***	+++	***	++	**	+
Castanopsis fargesii	***	+++	*	+	*	–	*	–
Cyclobalanopsis glauca	*	+	–	–	–	–	–	–
Lithocarpus harlandii	*	+	–	–	–	–	–	–
Camellia oleifera	***	+++	–	–	–	–	–	–
Total	High	High	Medium	Medium	Low	Low	Low	Low

[a] Tree abundance (Xiao and Zhang, unpublished data): (***) dominant (>80 fruiting individuals per ha); (**) common (20–80 fruiting individuals per ha); (*) rare (<20 fruiting individuals per ha); −, non-existing (no or few fruiting individuals per ha).

[b] Seed availability was estimated from seed traps (0.5 m² sample area) in primary and secondary stands (Xiao et al., 2001) and ground quadrates (1 m² sample area) in shrublands (Xiao and Zhang, 2004), the abundance of fruiting individuals and fruiting conditions (Xiao, personal observation): (+++) rich; (++) medium; (+) poor; (−) non-existing.

these rodents was similar among primary stands, secondary stands, shrublands and plantations ($X^2 = 1.99$, d.f. = 3, $P = 0.574$, χ^2-tests), though the dominant rodent species were slightly different among the four stand types (Table 2). In addition, at least four other rodent species were also captured in the same stands in the following years (2001–2003), e.g. Norway rats (*R. norvegicus*), South China field mice (*A. draco*), striped field mice (*A. agrarius*) and harvest mice (*Micromys minutus*) (Xiao and Zhang, unpublished data). The 11 rodents comprised the main seed-eaters of the large-seeded study species (with marked preference for *Castanopsis fargesii*, *L. harlandii* and *Camellia oleifera*, over *Q. variabilis*, *Q. serrata* and *C. glauca*) (Xiao et al., 2003a; Xiao and Zhang, 2004), and Edward's long-tailed rats were observed scatter-hoarding the tree seeds (Xiao et al., 2003a). Several native birds, notably Eurasian jays *Garrulus glandarius*, were also seed predators and potential seed dispersers, but they have small populations and may contribute relatively little to forest regeneration. Moreover, these birds seldom forage on the ground under the canopy (Xiao, personal observation).

3. Study species and methods

Six sympatric large-seeded species: *L. harlandii*, *Q. variabilis*, *Q. serrata*, *C. glauca*, *Camellia oleifera* and *Castanopsis fargesii*, were selected for this study because they

varied in seed mass, nutrient concentration, tannin concentration and seed coat thickness (but seed coat not included in data analysis, Table 3), but had overlapped seed rain periods. Seed chemical analysis was conducted in duplicate on a mixture of sound seeds ($n = 50$–100) for each seed species. Seed nutrient compositions, i.e. protein, fat, starch and tannin, were provided by Center of Grain Quality of Ministry of Agriculture, China, and caloric value was measured by Bomb Calorimeter (PARR 1281) at the Institute of Zoology, CAS. In this study, seed value is high for larger seeds, e.g. *L. harlandii* and *Q. variabilis*, and high fat seeds, i.e. *Camellia oleifera*, according to energetic value per seed species, i.e. dry mass (mean, g) times caloric value (J/g) (Table 3). Handling time (s) per seed, adopted from Xiao et al. (2003a,b), are related to seed mass and seed coat hardness (Table 3). The main seed rain periods of these six tree species overlap in October (Table 3), with little difference in peak time (Xiao et al., 2001, 2004c; Xiao, 2003, personal observation). Seed abundance varied among the four stand types based on species abundance and fruiting conditions: high in primary and secondary stands, and low in shrublands and plantations (Table 1, see Xiao et al., 2001, 2004a,c).

4. Seed predation and removal

The four stand types chosen as experimental sites in this study were: a primary stand (direction, east; 1.5 ha), a secondary stand (direction, north; 2.0 ha), a shrubland (direction, north; 0.5 ha)

Table 2
Number of small rodents captured ($n = 150$ trap nights) in late October 2000 (from Xiao et al., 2002)

Rodent species	Body mass (g)	Primary stand	Secondary stand	Shrubland	Plantation
Niviventer confucianus	<100	9	6	5	–
N. fulvescens	<100	3	4	3	4
Berylmys bowersi	200–400	5	–	–	1
Leopoldamys edwardsi	200–500	2	2	2	1
Apodemus latronum	<30	–	–	1	2
Apodemu chevrieri	<70	–	1	–	–
Rattus nitidus	100–200	2	5	3	7
Total		21	18	14	15

Table 3
Some ecological and innate traits of the seeds among target large-seeded species. Seed chemical analysis was conducted in duplicate on a mixture of sound seeds ($n = 50$–100) for each seed species

Species	Fruiting	Seed mass (g)		Protein (%)	Fat (%)	Starch (%)	Tannin (%)	Caloric (kJ/g)	Seed coat	Handling	
		Fresh	Dry							kJ/seed	time (s)/seed[a]
L. harlandii	October–December	4.56	3.14	5.80	0.91	37.66	1.34	17.11	Hard	53.73	772
Q. variabilis	September–December	2.42	1.71	5.92	3.94	54.17	11.7	17.63	Soft	30.15	205
Q. serrata	September–December	0.97	0.77	6.07	3.02	54.01	10.6	17.26	Soft	13.31	82
C. glauca	October–December	0.95	0.47	4.80	1.88	55.42	11.1	17.00	Soft	7.99	76
Camellia oleifera	September–November	0.90	0.47	10.91	51.79	11.74	0.1	29.56	Soft	13.89	53
Castanopsis fargesii	October–December	0.46	0.31	4.90	1.22	67.65	0.2	17.03	Soft	5.28	34

See details for seed chemical analysis in text.

[a] Handling time (s) per seed, adopted from Xiao et al. (2003a,b), was the whole time that Edward's long-tailed rats (*Leopoldamys edwardsi*) consume a given seed.

and a plantation (direction, north; 1.0 ha). These four stands were at least 500 m from each other. In each experimental site, 10 cafeteria plots were spaced 10–20 m apart along a transect line over 150 m long (see below). When the seeds of study species were available in October, we collected them from the ground or directly from fruiting plants, and used water floatation to distinguish between sound and insect-damaged/empty seeds. Then we randomly selected sound seeds for experimental use. At each cafeteria plot, we placed 60 seeds, i.e. 10 seeds for each seed species on the ground within an area of 1 m^2 (total 2400 seeds, $n = 100$ per species in each experimental period). The experiment was conducted during two periods: during the peak of seed rain (Peak, October 27–November 17) and during the end of seed rain (End, November 30–December 8). On 1–4, 6, 8, 10, 12, 16, 20th days after seed exposure, we examined the proximate fates of the released seeds at each cafeteria plot: eaten in situ, remaining or removed. The ultimate fates of the removed seeds were not determined in this study.

5. Data analysis

Three variables were considered for data analysis: (1) the time (days) to seed harvest, (2) the proportion of seeds eaten in situ or (3) the proportion of seeds removed. Repeated measure ANOVA was used to test the differences of each variable with season as the within-subject factor and seed species and stand as the between-subject factors, because the experiments were repeated during the peak period and the end period within the same fruiting season. The time-to-harvest was natural-log-transformed and proportions were arcsine-transformed to attain normality. For all the data across stands and seasons, we calculated Spearman's correlation coefficient ($n = 48$) between innate seed traits (seed mass, fat, protein and starch content, tannin content, energetic value per seed and handling time per seed, Table 3) and the mean time-to-harvest per species, or the total proportion of seeds removed or eaten in situ (these proportions were pooled per species).

6. Results

Nearly all seeds were removed or eaten in situ by the end of each experimental period, except for several *Q. serrata* and *C.*

glauca seeds remaining at the peak of seed rain in the primary and secondary stands. Repeated measures ANOVA indicates that the fruiting season, seed species and stand all had a strong effect on all three-response variables: time-to-harvest, proportion of seeds eaten in situ and the proportion removed as discussed below (Table 4).

6.1. Effects of seed species

For any stand or season, the time to seed harvest was shortest for *Castanopsis fargesii* (the smallest seeds with lower tannin), second for *L. harlandii* and *Camellia oleifera*, then for *Q. variabilis*, and the longest for *Q. serrata* and *C. glauca* (Fig. 1). For any stand or season, the proportion of *L. harlandii* and *Camellia oleifera* seeds eaten was much lower (<5%), but the proportion of seeds removed was much higher, while *Castanopsis fargesii*, *Q. serrata* and *C. glauca* seeds had higher levels of destruction (>10%) but lower levels of removal (Fig. 2).

Spearman's correlation showed that: (1) only tannin concentration was negatively correlated with the mean time-to-harvest ($r = -0.314$, $P = 0.03$); (2) dry seed mass was significantly correlated with the total proportion of seeds removed ($r = 0.332$, $P = 0.021$) or eaten ($r = -0.349$, $P = 0.015$), though fresh seed mass was marginally correlated with the total proportion of seeds removed ($r = 0.258$, $P = 0.077$) or eaten ($r = -0.273$, $P = 0.06$) (Table 5). This supports our prediction that seed mass is positively correlated with seed removal, but negatively with seed eaten in situ. In addition, starch content was negatively correlated with seed removal ($r = -0.547$, $P < 0.001$), but positively with seed eaten in situ ($r = 0.563$, $P < 0.001$) (Table 5).

6.2. Effects of stand

For either season, the time-to-harvest was longer in the primary stand than in any other stand for *Q. variabilis*, *Q. serrata* and *C. glauca*, but the time-to-harvest varied a little in all stands (except the plantation) for the other three species (*L. harlandii*, *Castanopsis fargesii* and *Camellia oleifera*, Fig. 1). For any seed species and season, the removal proportion was higher in the primary or secondary stand than in the shrubland

Table 4
Repeated measures ANOVA of the effects of season (within-subject factors) and seed species and stand (between-subject factors) on three variables: time-to-seed-harvest, the proportion of seeds eaten in situ and the proportion of seeds removed

Within-subject effects					Between-subject effects				
Source	d.f.	MS	F	P	Source	d.f.	MS	F	P
Time-to-seed-harvest									
Season	1	413.013	129.75	<0.001	Species	5	236.23	58.759	<0.001
Season × species	5	247.451	77.738	<0.001	Stand	3	203.92	50.722	<0.001
Species × stand	3	534.324	167.86	<0.001	Species × stand	15	121.13	30.129	<0.001
Season × species × stand	15	107.042	33.628	<0.001	Error	2376	4.020		
Error	2376	3.183							
The proportion of seeds eaten in situ									
Season	1	268.502	58.650	<0.001	Species	5	94.377	18.562	<0.001
Season × species	5	34.217	7.474	<0.001	Stand	3	167.491	32.942	<0.001
Species × stand	3	38.358	8.379	<0.001	Species × stand	15	10.726	2.110	0.011
Season × species × stand	15	10.133	2.213	0.007	Error	216	5.084		
Error	216	4.578							
The proportion of seeds removed									
Season	1	343.408	69.298	<0.001	Species	5	107.96	20.309	<0.001
Season × species	5	46.948	9.474	<0.001	Stand	3	142.45	26.797	<0.001
Species × stand	3	31.081	6.272	<0.001	Species × stand	15	11.774	2.215	0.007
Season × species × stand	15	9.147	1.846	0.030	Error	216	5.316		
Error	216	4.956							

or the plantation, while the reverse was true for the eaten proportion (Fig. 2). The eaten proportion in the primary stand was lowest for *L. harlandii* and *Camellia oleifera* seeds (<1%), followed by *Q. variabilis*, *Q. serrata*, *Castanopsis fargesii* and *C. glauca* in both seasons (Fig. 2). Eaten proportions in the secondary stand remained low or increased slightly, and increased significantly in remaining stands following a similar hierarchy in both seasons (Fig. 2).

6.3. Effects of season

For any seed species or stand (except the plantation), the time-to-harvest was longer at Peak than at End (Fig. 1). The time-to-harvest was much longer for *Q. variabilis*, *Q. serrata* and *C. glauca* at Peak than at End, but the time-to-harvest was similar between two seasons for *L. harlandii*, *Castanopsis fargesii* and *Camellia oleifera* (Fig. 1). The time-to-harvest in
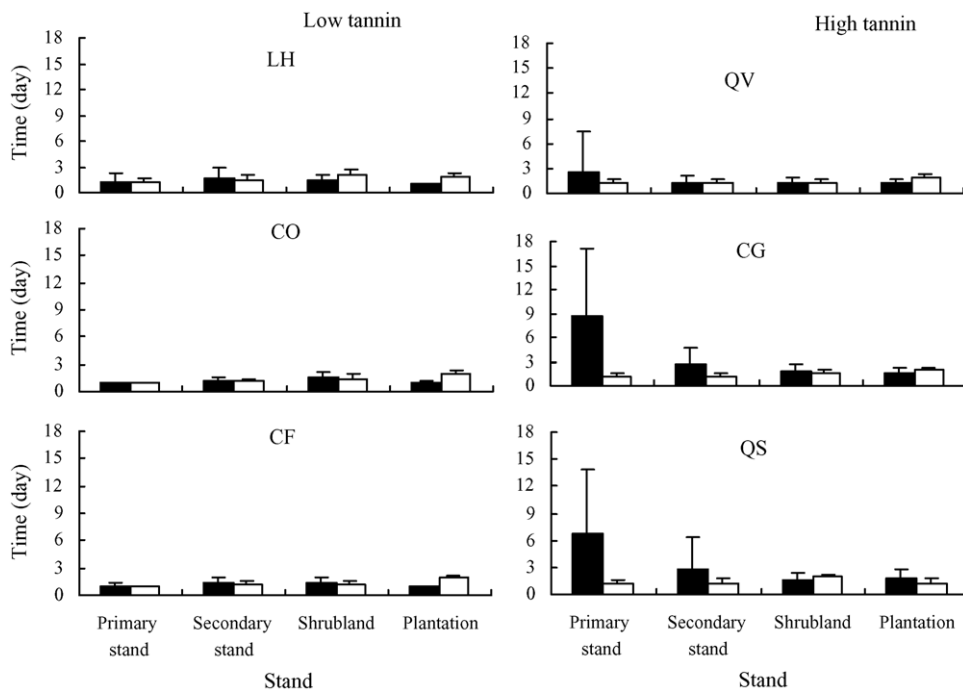

Fig. 1. Differences in the time (days) to harvest among six large-seeded species: *Castanopsis fargesii*, *Camellia oleifera*, *Cyclobalanopsis glauca*, *Quercus serrata*, *Q. variabilis*, and *Lithocarpus harlandii* across stands (a primary stand, a secondary stand, a shrubland and a plantation of *Cryptomeria fortunei*) and seasons (the peak and the end of seed rain).
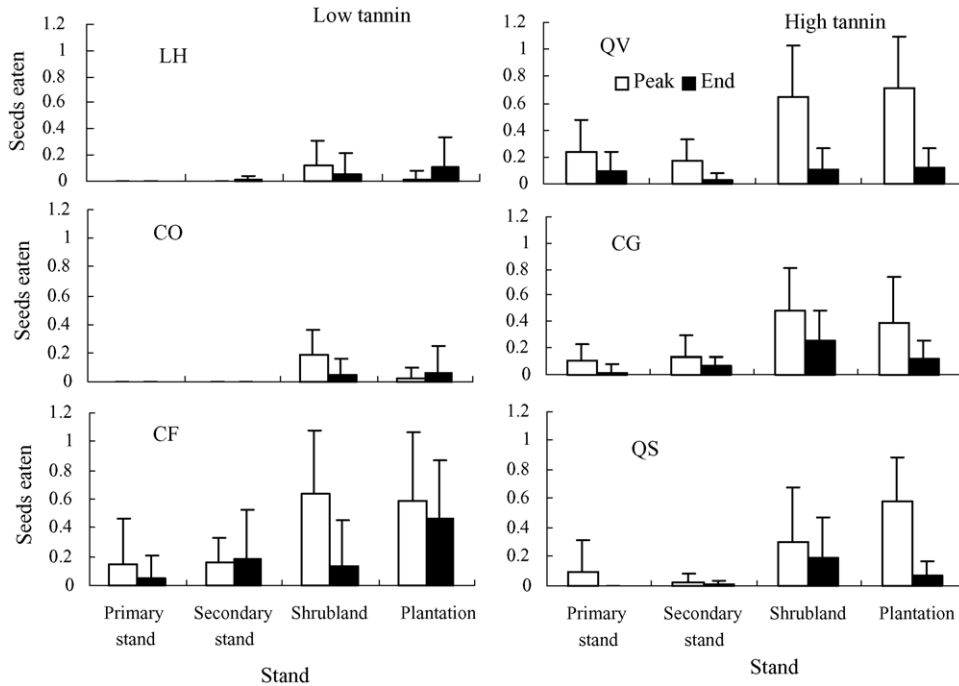
Fig. 2. Post-dispersal seed predation (only including eaten in situ here) among six large-seeded species: *Castanopsis fargesii*, *Camellia oleifera*, *C. glauca*, *Q. serrata*, *Q. variabilis*, and *L. harlandii* across stands (a primary stand, a secondary stand, a shrubland and a plantation of *Cryptomeria fortunei*) and seasons (the peak and the end of seed rain). The part of seed removal was not presented here because the sum of seed eaten in situ and seed removal nearly equal to 100%.

the resource rich primary stand (Table 1) in the peak season was shortest for *Castanopsis fargesii*, second for *L. harlandii* and *Camellia oleifera*, then for *Q. variabilis*, and the longest for *Q. serrata* and *C. glauca* (Fig. 1). Time-to-harvest in remaining stands and seasons was significantly shorter for all species, but showed a similar hierarchy (Fig. 1). For all stand or seed species, the proportion of seeds eaten was higher at Peak than at End (Fig. 2), but the reverse was true for the removal proportion.

7. Discussion

In the study site, small rodents were the main granivorous animals feeding on seeds on the ground based on seed fragments of the eaten seeds, while birds were seldom

observed to feed on seeds on the ground (Xiao et al., 2001, 2002, 2003a,b; Xiao, 2003; Xiao and Zhang, 2004). These results indicate small rodents are primarily responsible for seed predation and removal observed in this habitat. Our results show that time-to-harvest, and the proportions of seeds eaten in situ or removed varied greatly among seed species in relation to innate seed traits, with some variation occurring among stands and seasons.

7.1. Effects of innate seed traits

Our results illustrate two main points about the effects of innate seed traits on seed predation and removal by rodents. First, the time-to-harvest was correlated to innate seed traits. Indeed, for both stands and seasons, *Castanopsis fargesii* with

Table 5

Spearman's correlation coefficient ($n = 48$) between innate seed traits and the mean time-to-harvest, or the total proportion of seed removal (removed) or eaten in situ (eaten)

Seed traits	Time-to-harvest		Removal		Eaten	
	r	P	r	P	r	P
Fresh seed mass	0.263	0.071	0.258	0.077	−0.273	0.060
Dry seed mass	0.215	0.142	0.330	0.022[**]	−0.345	0.016[*]
Protein	−0.108	0.465	0.332	0.021[**]	−0.349	0.015[*]
Fat	−0.082	0.582	0.119	0.420	−0.131	0.374
Starch	0.017	0.908	−0.547	<0.001[**]	0.563	<0.001[**]
Tannin	0.314	0.030[*]	−0.232	0.112	0.217	0.139
Energetic value per seed	0.063	0.668	0.523	<0.001[**]	−0.526	<0.001[**]
Handling time per seed	0.263	0.071	0.258	0.077	−0.273	0.060

See details in data analysis.
[*] $P < 0.05$.
[**] $P < 0.001$.

lower tannin concentration, *L. harlandii* with the largest size and *Camellia oleifera* with high fat concentration, were harvested more quickly than the apparently less preferred seeds *Q. variabilis*, *Q. serrata* and *C. glauca* with higher tannin concentration, which supports Hypothesis I that high fat or large seeds are harvested more quickly. Second, seed value, e.g. large seed size and high starch or fat content, was most important in determining whether a given seed was eaten in situ, or removed by small rodents. For both stands and seasons, large (*L. harlandii* and *Q. variabilis*) or high fat seeds (*Camellia oleifera*) had higher levels of removal and lower levels of instant consumption than small seeds (*Castanopsis fargesii*) or seeds with higher tannin concentration (e.g. *Q. serrata* and *C. glauca*). This indicates that what to eat or remove are more likely to be determined by innate seed traits, especially seed size (Hypothesis II). Our results do not support the hypothesis that larger seeds have higher instant predation rates than smaller seeds (cf. Moles et al., 2003). The act of dispersal begins with removal of viable seeds. Larger seeds have a higher probability of being removed intact, while smaller seeds are more likely to be instantly consumed by granivorous rodents. Why?

During the foraging process, granivorous animals (e.g. rodents) often face two types of decision-making: (1) whether to consume a given seed or not and (2) if they decide to consume it, whether to eat it or carry it elsewhere (see Shimada, 2001). Therefore, for a given seed, there are often two fates when it is harvested: eaten or removed. Logically, larger seeds have a greater nutritional value (Grubb and Burslem, 1998), and thus are more attractive to seed-caching rodents (Smith and Reichman, 1984; Vander Wall, 1995; Jansen et al., 2002). In general, the marginal return from caching small seeds would be very low when a rodent encounters a seed. Therefore, it is possible that seed-caching animals prefer to remove and then cache larger seeds or higher-value seeds for later use, but consume smaller seeds immediately to compensate the energetic cost during the foraging process. Increasing field evidence indicates that large or high-value seeds are more likely to be removed and cached more often than smaller ones among different plant species (Hurly and Robertson, 1987; Vander Wall, 1995; Forget et al., 1998; Xiao, 2003), and within the same species (Hallwachs, 1994; Jansen et al., 2002, but see Brewer, 2001). Though we did not track the fates of the removed seeds in this study, our other studies tracking individual seeds with coded tin-tags in the same study site over 5 years found that larger seeds (*L. harlandii* and *Q. variabilis*) or high fat seeds (*Camellia oleifera*) have lower instant consumption, higher seed removal and seed-caching than smaller seeds (*Q. serrata*, *C. glauca* and *Castanopsis fargesii*) (Xiao, 2003, unpublished data; Xiao et al., 2004a,b, 2005).

In addition, other seed traits may also affect the intensity of seed predation and seed removal including caching. Seed-eating rodents often prefer seeds with high fat concentration (Kerley and Erasmus, 1991; Jansen and Forget, 2001; Xiao et al., 2003a, this study). Seeds with higher tannin concentration (e.g. *Q. variabilis*, *Q. serrata* and *C. glauca* in this study) or other secondary compounds may reduce the attractiveness to

seed-eating rodents, and they often have higher instant consumption and a lower removed/cached rate (e.g. Steele et al., 1993; Hulme and Hunt, 1999; Shimada, 2001; Zhang et al., 2004, but see Smallwood et al., 2001). The seeds with a hard husk (e.g. *L. harlandii* in this study) are more likely to be removed or cached because instant consumption incurs an increased predation risk due to a longer handling time (Xiao et al., 2003a; Xiao, 2003, see Jacobs, 1992; Hadj-Chikh et al., 1996).

7.2. Consistencies of seed predation and removal

Our results confirm other observations by Kollmann et al. (1998) that seed predation and removal are consistent among seasons and sites (Hypothesis III), especially for the more preferred species (e.g. *Castanopsis fargesii*, *L. harlandii* and *Camellia oleifera*), though community level seed availability has some effect on the foraging patterns of seed-eating rodents. This also supports our assumption that seed preferences of seed-eating rodents are more related to innate seed traits (Hypothesis II, see above for details). Hulme and Hunt (1999) also indicated that seed preferences by seed-eating rodents remain relatively stable across sites with different seed availability.

However, our results indicate that seed predation based on time-to-harvest may not represent real seed predation. Seeds are eaten in situ, left in situ, or removed. Removed seeds, especially larger seeds, are likely to be cached, indicating that seed disappearance is not equivalent to seed predation (e.g. Vander Wall, 1995, 2003; Forget et al., 1998; Zhang and Wang, 2001; Jansen et al., 2002; Li and Zhang, 2003; Xiao et al., 2004a,b). Therefore, seed harvest rate (including eaten and removed proportions) is not equal to seed predation rate (Jansen, 2003; Xiao, 2003). On the other hand, the time-to-harvest or disappearance of seeds are also affected by seed availability. For example, time-to-harvest was significantly different at Peak for all stands, though it was similar (less than 3 days) at End (Fig. 1). We assume the rapid and relatively synchronous onset of seed availability of all species that occurred at the peak in the primary stand in October was sufficiently abundant to satiate the existing rodent populations. These relatively well-fed rodents encountering a cafeteria plot in the primary stand would have had previous experience with some, if not all, of the seed choices available. The eat-remove-ignore decision process is thus predisposed to favor the remove-ignore components due to their presumed already well-fed condition. The rapid removal of *L. harlandii* (53.7 kJ/seed), *Camellia oleifera* (13.9 kJ/seed) and *Castanopsis fargesii* (5.3 kJ/seed) indicate these low tannin resources merit hoarding to a greater extent that the other three higher tannin laden species. Some *Castanopsis fargesii* are also eaten. We suggest this is due to their significantly lower caloric value/seed, which poses the dilemma of being of limited value to hoard but too valuable to ignore. This hierarchy is also reflected in the secondary stand. The significantly more rapid removal and increased consumption of seeds of all species in the low seed resource shrub and plantation stands (Figs. 1 and 2) indicate resident rodents were not as satiated as those in other stands. This

observation needs further tests because we have only one replicate for each stand. *Castanopsis fargesii*, the smallest seed in size and caloric value, was more readily eaten than other species, followed closely by *C. glauca*, and more distantly by the remaining species (Fig. 2). These results indicate seed size, caloric value/seed and tannin content interact with the degree of resource satiation in the rodent populations to largely explain rates of seed removal and amounts of consumption. These factors combine to result in dispersal of each species. Using these criteria, the six species were ranked 1–6 and the rank total for each species was obtained as an indicator of their rates of removal. This resulted in *L. harlandii* > *Camellia oleifera* > *Q. variabilis* > *Q. serrata* > *Castanopsis fargesii* = *C. glauca* (Fig. 2).

Examination of the relative abundance of the six tree species in the primary stand shows *Q. serrata* (4), *C. glauca* (5.5) and *L. harlandii* (1) to be lowest, *Q. variabilis* (3) to be intermediate and *Camellia oleifera* (2) and *Castanopsis fargesii* (5.5) to be most abundant. The number in parentheses shows the rank indicating the rate of removal (1 = highest) calculated above. *L. harlandii*, low in actual abundance but high in perceived rate of removal, and *Castanopsis fargesii*, high in actual abundance and low in perceived rate of removal, show that removal alone will not explain relative abundance of trees at maturity. We note that, compared to other seeds, *L. harlandii* is among the poorest provisioned in fat, starch and protein content; the large size may reduce rodent species that can disperse them into the most suitable microhabitats; and the hard seed coat may delay germination. *Castanopsis fargesii*, conversely, is the highest in starch content; more rodent species can access this order of magnitude smaller seed; and it has a softer seed coat. These and other factors must also play a role in determining actual species distribution and abundance of trees in natural stands.

In conclusion, our results show that innate seed traits, especially seed size, are important in determining whether a given seed is eaten or removed, whereas seed abundance over time and space might affect the intensity of seed predation and removal. This also implies that seed selection by granivorous rodents have the potential to influence the evolution of innate seed traits (e.g. seed size, nutrient quality, chemical defenses), and vice versa. Rodent survival and reproduction is closely linked to the innate traits of seeds, and whether they are eaten or cached directly influences the potential establishment of plants. Innate seed traits are under genetic control in each plant species and the balance between benefits (seed dispersal) and costs (seed predation) plays a role in their evolution. How these innate seed traits evolve to balance seed predation and dispersal by granivorous rodents or other animals should be further investigated.

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