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Seed size and number make contrasting predictions on seed survival and dispersal dynamics: A case study from oil tea *Camellia oleifera*

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ABSTRACT

Seed size and number vary greatly both within and among plant individuals, populations or species. However, we know little about how individual variation in seed size and number relates to seed survival and dispersal dynamics in animal-dispersed plants. Based on the large-seed hypothesis and the predator satiation hypothesis, we developed a synthetic framework and testable predictions for how seed size and number interact to predict seed survival-dispersal patterns at the seed and tree scales, and tested for these effects using rodent-dispersed oil tea, *Camellia oleifera*. Our results showed that seed size and number varied considerably at both fruit and tree scales, and mean seed size for each fruit was negatively correlated with the number of seeds per fruit. We placed groups of individual-weighed seeds in a way that mimicked seed size and number from individual trees and tracked the fate of these seeds. This showed that seed survival in situ at source trees decreased with increasing seed size, but seed dispersal and the subsequent survival of dispersed seeds increased with larger seed size. In addition, seed survival in situ at source trees increased with larger seed number per tree, but the proportion of dispersed seeds decreased as seed number per tree increased. We demonstrate that individual variation in seed size and number have strong but contrasting effects on seed survival and seed dispersal in oil tea. Moreover, these two factors are not independent in their effects on seed survival at the source tree, but after dispersal, the size of individual seeds may be more important in determining seed survival or further handling by scatterhoarding animals.

1. Introduction

Seed dispersal by animals is a critical process for plant recruitment and many different abiotic and biotic processes may result in a relationship between seed survival and dispersal distance (Janzen, 1971; Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Moles and Westoby, 2006). In animal-dispersed plants, the probabilities of seed survival and dispersal depend not only on the foraging and movement of seed dispersers and predators, but also on seed size and number (Vander Wall, 2010). It is well known that seed size and number vary greatly both within and among plant individuals, populations or species (Leishman et al., 1995; Herrera, 2009). In plants, seed size-number trade-offs provide a classic example of an evolutionary tradeoff resulting from reproductive allocation, with selection favoring either few large seeds or many small seeds (Smith and Fretwell, 1974; Shipley and Dion, 1992; Venable, 1992; Jakobsson and Eriksson, 1999). Nevertheless, how seed size and number interact to determine seed survival and dispersal dynamics is poorly understood in animal-dispersed plants.

Both interspecific and intraspecific variation in seed size play significant roles in seed dispersal, seed germination and seedling recruitment (Jordano, 1995; Rees, 1996; Westoby et al., 1996; Alcántara and Rey, 2003; Gómez, 2004; Jansen et al., 2004; Moles and Westoby, 2004; Martínez et al., 2007; Lönnberg and Eriksson, 2012, 2013; Sobral et al., 2014). As predicted by the large-seed hypothesis (Sork, 1993), selection for larger seeds may be favored in the habitats where larger seeds better withstand diverse abiotic and biotic risks, including drought, shade, seed predation and competition (Leishman, 2001; Gómez, 2004; Moles and Westoby, 2006; Baraloto and Forget, 2007; Muller-Landau, 2010). However, how seed survival and dispersal benefit from variation in seed size is not understood for animal-dispersed plants (Jordano, 1995; Alcántara and Rey, 2003; Gómez, 2004; Martínez

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et al., 2007). Seed-size variation could be advantageous to an individual tree if large seeds are more likely to be dispersed and hoarded by seed dispersers such as scatter-hoarding rodents (Smith and Reichman, 1984), while smaller seeds are more likely to escape from seed predators (Moles et al., 2003). Growing evidence has shown that scatter-hoarding rodents prefer to hoard larger seeds over smaller seeds because larger seeds are more profitable (Forget et al., 1998; Vander Wall, 2002, 2003; Jansen et al., 2004; Xiao et al., 2004, 2005). Therefore, the large-seed hypothesis applies when dispersal efficiency and distance increase with seed size (Jansen et al., 2004).

Many perennial plant species show large annual variation in seed number that results in the production of large seed crops during some years, interspersed with other years of low seed crops (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). According to the predator-satiation hypothesis, large seed crops enhance pre-dispersal seed survival by increasing seed escape from seed predators during high-seed years compared to that during low-seed years (Janzen, 1971; Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). However, other studies illustrate that large seed crops can enhance scatter-hoarding or increase dispersal distances during high-seed years compared with low-seed years (the predator-dispersal hypothesis, Vander Wall, 2002). Our recent long-term field study of oil tea supports the predator-satiation hypothesis rather than the predator-dispersal hypothesis (Xiao et al., 2013). We found that specifically, pre-dispersal survival of oil tea seeds increased with increasing seed abundance, but seed dispersal and subsequent survival were much higher when annual seed abundance was relatively low. However, it is rarely known whether seed number produced by individual trees can influence seed dispersal and survival dynamics in some masting plants that rely on animal seed dispersal.

Oil tea (*Camellia oleifera*), a rodent-dispersed tree species native in China, show large variation in seed size and number both with and among individual trees (Xiao et al., 2013; this study). We used this species to examine individual variation in seed size and number; and to test for the relationships between seed survival and dispersal as a function of seed size (individual seeds) and number (individual trees). Based on the large-seed hypothesis and the predator-satiation hypothesis, we presented a synthetic mechanism to understand how seed survival-dispersal patterns differ at the seed and tree scales in animal-dispersed plants that show considerable variation in seed size and number (Fig. 1). We tested the following three predictions: (1) At the fruit or tree scale seed size and number are negatively related due to the intrinsic constraint in seed/fruit packaging or the seed size-number tradeoffs in plants (Fig. 1A). (2) Larger seeds are more likely to be hoarded and then survive after dispersal from the parent tree, whereas smaller seeds have a higher probability escaping from seed predation and then surviving under the source trees (Fig. 1B). This is consistent with the large-seed hypothesis. (3) Seeds produced by individual trees with small-crops are more likely to be hoarded and survive after dispersal, whereas seeds from trees with large-crops survive better under the source trees, as predicted by the predator satiation hypothesis (Fig. 1C). In addition, we also expected that seed size and seed number may interact to influence seed survival and dispersal dynamics since seed size selection is largely affected by seed availability (Jansen et al., 2004).

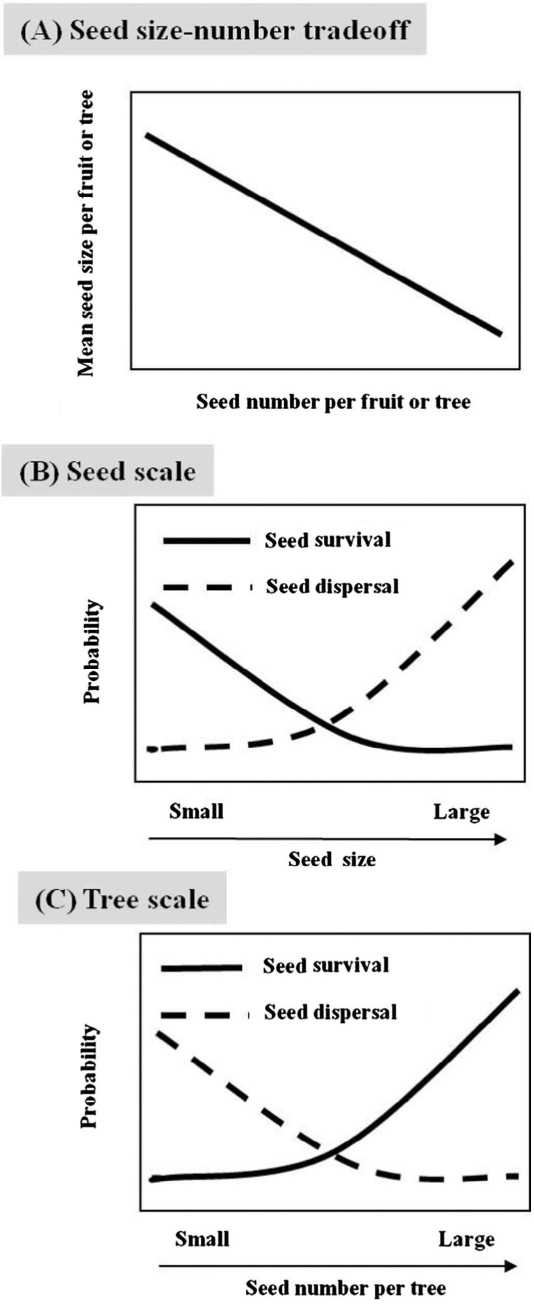

Fig. 1. A testable framework for the seed size-number tradeoff and related predictions on seed survival and dispersal as a function of seed size (seed scale) and seed number (tree scale). (A) Seed size-number tradeoffs predict that seed size and number have a negative relationship at the tree or fruit scale. (B) The seed survival-dispersal patterns at the seed scale predict that larger seeds are more likely to be hoarded and dispersed by scatterhoarding seed dispersers, whereas smaller seeds are more likely to escape seed predation and have higher seed survival in situ at the source tree (the large-seed hypothesis). (C) The seed survival-dispersal patterns at the tree scale predict that large seed number per tree favors seed survival in situ based on the predator satiation hypothesis, whereas small seed number per tree favors scatterhoarding and seed dispersal.

2. Materials and methods

2.1. Sites and species

Field work was conducted in the Banruosi Experimental Forest (700–1000 m, 31°4′N, 103°43′E) in Dujiangyan City, Sichuan Province, Southwest China. The site is in the subtropical zone, with a mean annual temperature of 15.2 °C, and annual precipitation of 1200–1800 mm. The weather is often cloudy and foggy, with 800–1000 mean annual h of sunshine and mean annual relative humidity $\geqslant 80\%$. Vegetation at the study site is subtropical evergreen broad-leaf forest. Common tree species include *Castanopsis fargesii*, *Quercus variabilis*, *Q. serrata*, *Lithocarpus harlandii*, *Cyclobalanopsis glauca*, *Pinus massoniana*, *Acer catalpifolium*, *Phoebe zhennan*, and

C. oleifera. The study site is a mosaic of isolated and fragmented small stands caused by agricultural development, highways and villages. Oil tea was widespread in the subtropical broad-leaved evergreen forests (altitude 700–900 m) at the study site, but current populations exist mainly in some old-growth stands and secondary stands. Our previous studies revealed that Edward's long-tailed rats (*Leopoldamys edwardsi*) scatter-hoarded oil tea seeds, whereas the other rodent species rarely scatter-hoarded oil tea seeds (Xiao et al., 2003; Chang and Zhang, 2011).

Like other *Camellia* species, oil tea is a broad-leaved, evergreen shrub or short tree. They are widespread in subtropical forests of south and southwest China. Oil tea seeds have high fat concentration (>50%), which is extracted for cooking oil. Oil tea is pollinated by bees, butterflies and flies, and its flowering coincides with fruit-ripening, from September to December. After ripening, oil tea fruits capsule, which contains one to 15 seeds, typically dehisce on the tree and the seeds fall to the ground under or close to parent plants. Seed size and number vary considerably within and among trees at the study site (Xiao et al., 2013; this study).

2.2. Seed size and number

We measured seed size and number for each fruit on 60 oil tea trees separated at least 20 m from each other in a *Camellia*-rich forest at the study site (Fig. S1). The trees sampled were all of similar size and were marked and their seed crops measured each year since 2002 (Xiao et al., 2013). On September 20–26 of 2009, we collected all of the fruits from these marked plants before fruits and seeds fall to the ground. We counted fruits, and after dissecting each fruit, we counted the number of seeds and weighed each seed to within 0.01 g.

2.3. Seed survival and dispersal

We investigated the relationships between seed survival and dispersal as a function of seed size (individual seeds) and number (individual trees) (Fig. S1). In 2009, we created eight seed crop groups based on the seed number from the 60 trees we had sampled: 40 seeds, 80 seeds, 120 seeds, 160 seeds, 200 seeds, 240 seeds, 280 seeds and 320 seeds. Then we haphazardly chose three trees (total: 24 trees and 4320 seeds) from each seed crop group, and we also adjusted the total seeds of a given tree to attain the desired crop size. All the 24 trees were a subsample of the 60 sampled trees. We placed the seeds in each of three isolated stands with all the eight crop groups. The three isolated stands were used as site replicates and their vegetation was quite similar with common Fagaceae species (e.g. *Castanopsis* spp., *Quercus* spp.) and oil tea trees. Within a stand, source trees selected were at least 20 m apart along a single transect. All seeds were weighed individually and labeled with a numbered tag attached by a 10-cm long thin stainless steel wire (Xiao et al., 2006). The tagged seeds were placed on the ground under the canopy of each oil tea tree from which all fruits had been removed in mid-October.

The fates of the tagged seeds were recorded and for the details of the seed tracking procedure see Xiao et al. (2006, 2013). The fates of individual seeds were categorized at different dispersal stages: (1) at source trees, fate categories included *survival* in situ (non-dispersed and uneaten), *eaten* (seed fragments with dental marks found) or *removed*; (2) after removal, the seeds were categorized as cached (1st caches), eaten, or *missing* (not found); and (3) after recovery from 1st caches, the seeds was further categorized as re-cached in a secondary cache, eaten or missing. In addition, we also measured the distances to their source tree for the cached seeds at different caching sites using tape. During the following spring (late April), we surveyed all source trees and all previous cache sites to determine whether seeds had germinated.

2.4. Statistical analysis

Seed size variation was measured within and among trees, including mean seed size per fruit and mean seed size per tree. The variation of seed number was also compared within and among trees, including the total number of seeds per fruit and the total number of seeds for each tree. Linear mixed models were used to partition the among- and within-tree variance in mean seed size or seed number with fruit nested within tree as a random effect (Packages nlme and ape in R). Pearson correlation tests were used to test for relationships between seed size and seed number at the fruit and tree scale. Seed size was square-root transformed and seed number was $\log_{10}$ transformed to produce approximately normal distributions.

Based on the seed fate data, scatterhoarding rodents can affect seed survival and dispersal during each dispersal stage from source trees to caching sites: (1) at the source, including non-dispersed and uneaten seeds (i.e. seed survival in situ at the source trees), eaten seeds and removed seeds at the source trees; (2) after removal from the source trees, including seeds cached (1st caches) and eaten elsewhere; (3) after recovery from the first caches (2nd caches), including seeds re-cached and eaten somewhere; and (4) the final fates of all cached seeds, including those surviving from 1st and 2nd caches the following spring (i.e. seed survival at caches) and eaten somewhere. The above seed fates represented binary outcomes, so we analyzed them with generalized linear mixed models with binomial distribution (Package lme4 in R) for each of the above seed fate data. These analyses included seed size and number as fixed factors and stand as a random factor, including the interaction of the two fixed factors. We also used linear mixed models to test the effects of seed size and number on dispersal distance (log-10 transformed) of the cached seeds at 1st caches with stand as a random factor (Package nlme in R). As an alternative analysis to generalized linear mixed models or linear mixed models, we also used generalized additive models to explore the nonlinear relationships of each of the above seed fate data as a function of the two fixed factors (Package mgcv in R). Both generalized linear mixed models (or linear mixed models) and generalized additive models showed similar effects of both seed size and num-

Table 1
Summary of the effects of seed size and number on seed survival and dispersal during each dispersal stage based on generalized linear mixed models or linear mixed models. Fixed factors in bold had significant effects.

Dispersal stage and fixed factor	Estimate	SD	*z*/*t*	*P*
Seed survival at the source				
Intercept	−17.048	2.622	6.502	<0.001
Seedsize	**−3.054**	**1.388**	**2.200**	**0.0278**
Seednumber	**0.047**	**0.006**	**8.049**	**<0.001**
Seedsize * seednumber	**−0.018**	**0.005**	**3.413**	**<0.001**
Seed survival at caches				
Intercept	−5.389	0.772	6.983	<0.001
Seedsize	**1.011**	**0.352**	**2.874**	**0.004**
Seednumber	−0.001	0.002	0.610	0.542
Fate after removal from the source (1st caches)				
Intercept	−3.389	0.481	7.050	<0.001
Seedsize	**1.655**	**0.304**	**5.439**	**<0.001**
Seednumber	0.004	0.002	1.899	0.058
Seedsize * seednumber	**−0.004**	**0.001**	**2.824**	**0.0047**
Fate after recovery from 1st caches (2nd caches)				
Intercept	−2.167	0.811	2.672	0.008
Seedsize	0.650	0.354	1.837	0.066
Seednumber	−0.003	0.002	1.183	0.237
Dispersal distance of the cached seeds (1st caches)				
Intercept	0.216	0.277	0.781	0.435
Seedsize	**0.284**	**0.092**	**3.085**	**0.002**
Seednumber	**0.003**	**0.001**	**4.378**	**<0.001**

ber on each of the above seed fate data (Tables 1 and 2). The missing seeds during each dispersal stage were treated as missing values in all the models.

Linear mixed models, generalized linear mixed models and generalized additive models were carried out in the R program (version 3.0.2, R Development Core Team, 2013).

3. Results

3.1. Seed size and number within and among trees

We measured 754 fruits (4 fruits with no seeds were excluded from the analysis) and 2331 seeds from 51 sampled trees (another 9 trees had no seeds) in 2009. Over 73% of the 60 trees produce less than 40 seeds. Seed number per fruit varied considerably among the sampled trees with among-tree variance 34.4% and within-tree variance 65.6% ($F_{50,699} = 9.942$, $P < 0.001$) (Fig. 2A). Mean seed size also varied significantly among the sampled trees ($F_{50,699} = 18.05$, $P < 0.001$; among-tree variance 45.8% and within-tree variance 54.2%) (Fig. 2B and C). At the fruit scale (pooled for all sampled trees), mean seed size was negatively correlated with seed number per fruit ($r = -0.497$, $P < 0.001$) (Fig. 3A), but at the tree scale, seed number was positively correlated with mean seed size ($r = 0.337$, $P = 0.016$, $n = 51$) (Fig. 3B).

3.2. Seed survival and dispersal at the seed and tree scales

3.2.1. Fates at the source trees

Rodents harvested (either ate or removed) most of the tagged seeds. Only 6.4% of the tagged seeds ($n = 275$ seeds) were left at the source trees and survived there. The probability of seeds surviving in situ at the source trees was lower with increasing seed size ($z = 2.200$, $P = 0.028$) but was higher with larger seed number ($z = 8.049$, $P < 0.001$; Figs. 4A1 and 4A2; Table 2). In addition, seed size and number also had significant interacting effects on the probability of seeds surviving at the source trees (Table 1). Seeds removed from the source trees were larger than those eaten at the source trees (Fig. 5A).

3.2.2. Fates after removal from the source trees

14.6% of the removed seeds ($n = 452$ seeds) were found to be cached in 1st caches, whereas others were either eaten elsewhere or missing. Seed size and its interaction with seed number had strong effects on the probability of seeds cached at the first caches, but seed number only had a marginally negative main effect (Figs. 4C1 and 4C2; Tables 1 and 2). The significant interaction indicates a nonlinear relationship between seed number and size. Seeds in first caches were larger than eaten seeds after removal from the source (Fig. 5B). In addition, the dispersal distance of seeds in first caches positively related with both seed size and number (Figs. 4E1 and 4E2; Tables 1 and 2).

3.2.3. Fates after recovery from the first caches

We found that 9.1% of the seeds ($n = 39$ seeds) from the first cache were recached in 2nd caches, and others were either eaten elsewhere or missing. In addition, two seeds from the second

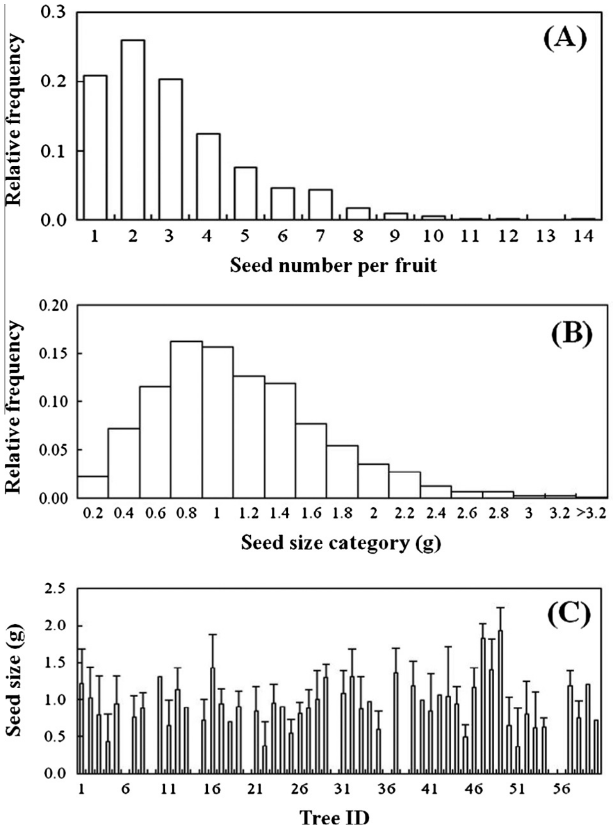

Fig. 2. Relative frequency of seed number per fruit (A), seed size (g, B) and mean seed size (g ± SD, C) from 60 sampled trees (nine of them had no fruits) of oil tea *Camellia oleifera* during 2009.

Table 2
Summary of the effects of seed size and number on seed survival and dispersal during each dispersal stage based on generalized additive models. Fixed factors in bold had significant effects.

Dispersal stage and fixed factor	edf	Ref. df	χ^2	P	R^2_{adj}
Seed survival at the source					0.334
s (seedsize)	**1.000**	**1.000**	**216.34**	**<0.001**	
s (seednumber)	**2.253**	**2.581**	**80.19**	**<0.001**	
Seed survival at caches					0.005
s (seedsize)	**1.001**	**1.001**	**8.281**	**0.004**	
s (seednumber)	1.044	1.086	0.333	0.599	
Fate after removal from the source (1st caches)					0.039
s (seedsize)	**1.634**	**2.011**	**63.563**	**<0.001**	
s (seednumber)	**1.636**	**1.995**	**8.236**	**0.016**	
Fate after recovery from 1st caches (2nd caches)					0.051
s (seedsize)	1.419	1.714	4.977	0.063	
s (seednumber)	1.797	2.180	4.799	0.105	
Dispersal distance of the cached seeds (1st caches)					0.079
s (seedsize)	**1.695**	**1.695**	**8.549**	**<0.001**	
s (seednumber)	**1.451**	**1.451**	**11.448**	**<0.001**	

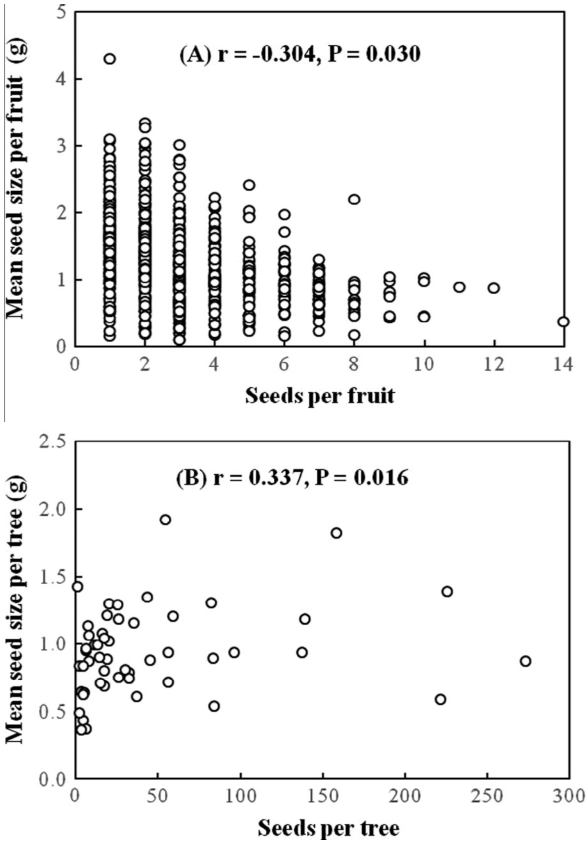

Fig. 3. Relationships between seed size and number of oil tea *Camellia oleifera* at the (A) fruit (all tree data pooled) and the (B) tree scales in 2009.

caches were recached in 3rd caches and one seed from a third cache was found at a fourth cache, but no seeds from these higher-order caches survived at the end of field survey. Compared to seed number, seed size had a positive, but non-significant effect on the probability of the cached seeds at the first cache being recovered and recached (Figs. 4D1 and 4D2; Tables 1 and 2). Seeds at the second caches were larger than seeds eaten after recovered from first caches (Fig. 5C).

3.2.4. Final survival of cached seeds

All 21 cached seeds surviving and germinating at the end of the field survey were from first caches. Seed size positively affected the probability of the cached seeds surviving (Figs. 4B1 and 4B2; Tables 1 and 2). On average, seeds surviving at the first caches (1.54 ± 0.56 g) were over twice the size of the seeds that survived in situ at source trees (0.64 ± 0.23 g) (Fig. 5D).

4. Discussion

Our study showed that seed size and number varied considerably within and among individual trees, and mean seed size of each fruit was negatively correlated with seed number per fruit. However, this negative relationship was not found at the tree scale. This confirms our first prediction about the seed size-number tradeoff at the fruit scale due to the intrinsic constraint in seed/fruit packaging. As reported in many other species (e.g. Mehlman, 1993; Simons and Johnston, 2000), the evolution of multi-seeded fruits in oil tea and other *Camellia* species may be favored since the production of more than one seed per fruit can reduce the parent packaging cost (Zhishu Xiao, unpublished data). Thus, multi-seeded fruit production by oil tea provides substantial within-tree variation in seed size and number. Our long-term survey (2002–2013) of the 60 marked oil tea trees showed large year-to-year variation in seed production (range: 0–1050 seeds per tree, the population mean coefficient of variation CV, 1.53) among different trees in the target population (Xiao et al., 2013; Zhishu Xiao, unpublished data). In addition, annual variation of mean seed size for each tree varied greatly (range, 0.25–2.70 g; population mean CV, 0.44; Zhishu Xiao, unpublished data). Recently, Koenig et al. (2009) did not find a negative relationship between acorn size and number in valley oaks *Quercus lobata* even after controlling for environmental conditions and tree-to-tree variation. This indicates that seed size-number tradeoffs are more complicated at the tree or population scales compared to those at the fruit scales (Moles and Westoby, 2006). The adaptive evolution of intraspecific variation in seed size and seed number are favored if such variation can enhance direct fitness benefits to the parent especially in unpredictable environments (McGinley et al., 1987; Herrera, 2009).

Our results provide sound support for the two seed survival-dispersal predictions illustrated in Fig. 1 relating to seed size (individual seeds, Fig. 1B) and seed number (individual trees, Fig. 1C). Our results showed that seed survival in situ at the source trees decreased with increasing seed size. However, seed dispersal and the subsequent survival of dispersed seeds increased with larger seed size. In addition, although seed survival at source trees increased with larger seed crops, seed dispersal and subsequent survival showed a decreasing trend when seed number per tree were larger. However, there was a significant effect only on the probability of seeds cached after being removed from the source trees. Interactions between seed size and number had a significant effect on seed survival at the source trees and seed dispersal after removal, but had no strong effects on seed dispersal and survival during later dispersal stages. This indicates that large individual variation in seed size and number play significant different roles in determining seed survival-dispersal patterns in oil tea and other animal-dispersed species (Fig. 1).

The size of individual seeds should affect whether a given seed is hoarded because seed size is related to food value for later use. In most cases, scatterhoarding rodents handle only one seed at a time (e.g. Jansen et al., 2004; Xiao et al., 2013; this study) though some scatterhoarding rodents like chipmunks with cheek pouches can simultaneously handle tens of small pine seeds (e.g. Vander Wall, 2002, 2003). Therefore, it is important to follow the fate of each individual seed. Consistent with our predictions, our field data revealed that seed size effects worked well across different dispersal stages from seedfall to seed germination (Figs. 3 and 4). Gómez (2004) also showed that smaller acorns of *Quercus ilex* survived better from rodent seed predation, though he did not track the final fate of removed acorns; removed acorns were larger and treated as consumed, though some acorns may be hoarded (dispersed) and survive to become seedlings (Gómez, 2004). In some bird-dispersed plants, seed size is subject to conflicting selective pressures from bird seed dispersers and rodent seed predators. Alcántara and Rey (2003) found the higher dispersal probability for smaller seeds of *Olea europaea*, but the probability of escape from post-dispersal seed predators increased with seed size. However, Martínez et al. (2007) showed an increase in seed dispersal but a decrease of seed survival after dispersal for larger seeds in *Crataegus monogyna*. By tracking the fate of individual seeds from six frugivore-dispersed plants at the same study site as the current study, Lai et al. (2014) identified three patterns of post-dispersal seed survival: large-seeded species with a hard seed coat (i.e. *Choerospoadias axillaries* and *Diospyros kaki var. silvestris*) had more seeds removed, cached and then surviving at caches, and they also had less seeds predated but a higher proportion of seeds surviving in situ at the source; medium-sized species with higher profitability

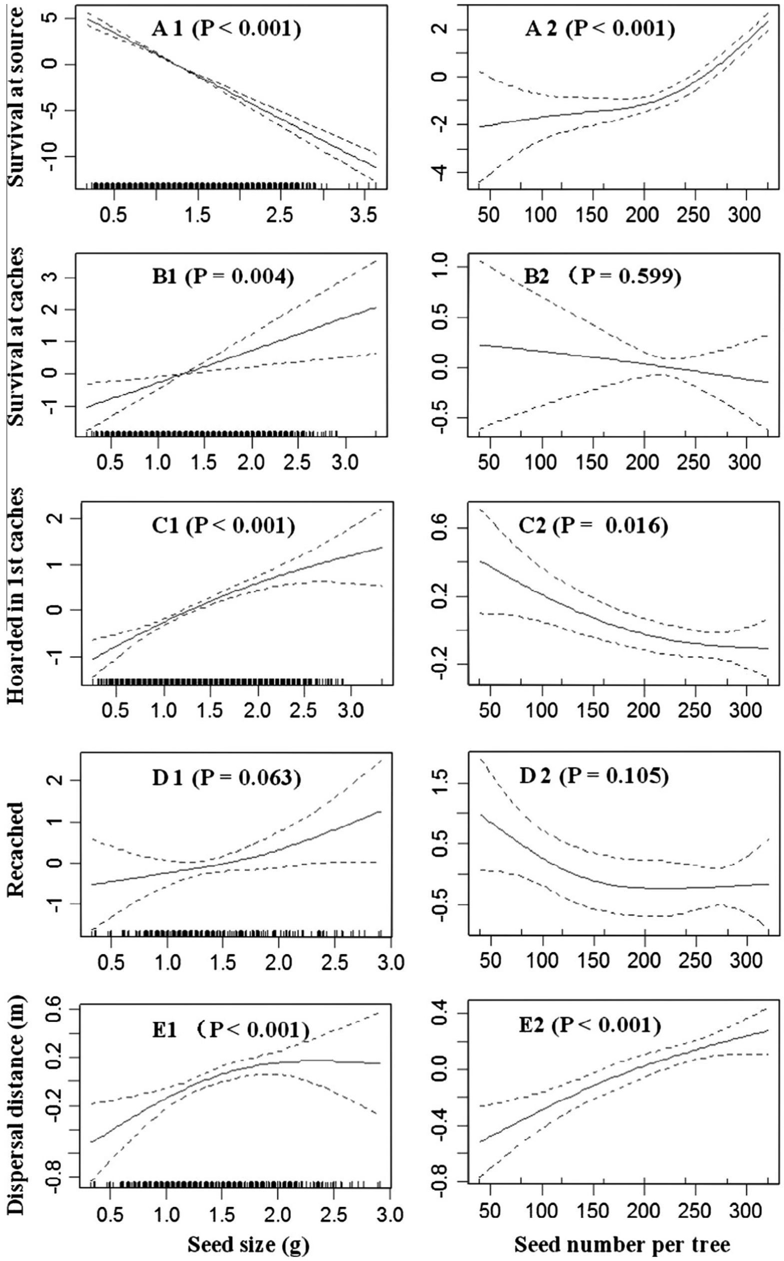

Fig. 4. The results (R-function) of generalized additive models for the relationships between seed size and seed fates (seed scale: A1–E1), and the relationships between seed number per tree and seed fates (tree scale: A2–E2) for oil tea *Camellia oleifera* during each dispersal stage. Dashed lines are 95% confidence bands for the predictions.

and thinner seed coat (i.e. *Phoebe zhennan* and *Padus braohypoda*) were first harvested and had the lowest probability of seeds surviving either at the source trees or at caches due to higher predation before or after removal; and small-seeded species with lower profitability (i.e. *Elaeocarpus japonicas* and *Cornus controversa*) had the highest probability of seeds surviving in situ at the source trees but the lowest probability of seeds surviving at caches due to lower predation at the source trees and lower hoarding at caches. Therefore, the evolution of large seed size appears to be favored for scatterhoarding-mediated seed dispersal at least at the seed scale, while the evolution of small seed size may be favored because of increased probability of escape from seed predation. Moreover, such seed survival-dispersal tradeoffs can be achieved at the seed scale within individual trees since there exists large intraspecific variation in seed size.

Unlike individual seeds, the effects of individual plants on seed survival and seed dispersal are quite different (Fig. 1). As predicted by the predator satiation hypothesis, synchronous production of large seed crops (i.e. mast seeding) from most of individual plants within a given population enhances escape from seed predation (Janzen, 1971; Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). Xiao et al. (2013) found that the probability of seed dispersal and subsequent survival was much higher when local seed abundance was relatively low. In this study, we found a similar pattern of seed survival and dispersal as a function of seed number from individual oil tea trees: an increase of seed survival at the source tree but a decrease of seed dispersal with increasing seed crop per tree. Though seed production may vary considerably among plant individuals and populations over time and space, Xiao et al. (2013) and the current study provide clear evidence to

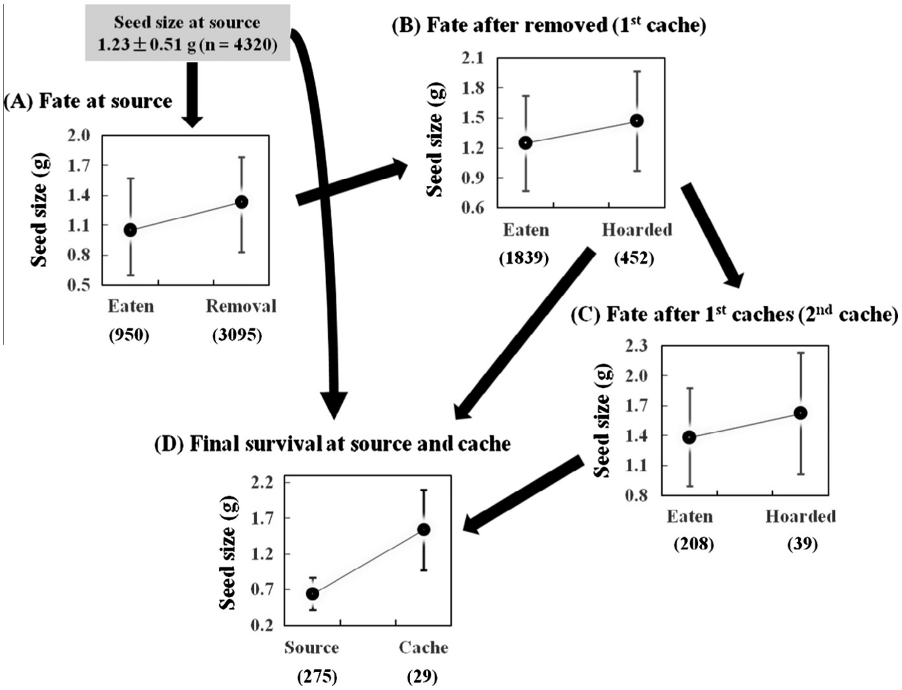

Fig. 5. Differences in seed size (g ± SD) between seeds eaten and dispersed of oil tea *Camellia oleifera* during each dispersal stage: (A) at source trees; (B) after removal from source trees (1st cache); (C) after 1st caches (2nd cache); and, (D) final survival at source trees and caches. Seed number is shown under each fate category in parentheses.

predict seed survival and seed dispersal dynamics in animal-dispersed plants based on the population- and tree-level seed production.

Whereas the ecological and evolutionary significance of seed size or seed number alone are often the focus of attention, their joint effects have been largely ignored. Here we found that the nonlinear interactions between seed size and seed number had strong effects on seed survival at the source trees and seed dispersal during seed removal. This indicates that seed size and number are not independent in their effects on seed survival and seed removal at the source tree. Jansen et al. (2004) also showed that seed abundance and seed size enhanced seed dispersal and subsequent survival of *C. procera*. They found that during seed removal, seed size selectivity by scatterhoarding rodents was greater under seed abundance. However, both Jansen et al. (2004) and this study showed that the seed size-number interactions had no strong effects on seed dispersal and subsequent survival at any other dispersal stage after seed removal. This indicates that after dispersal, the size of individual seeds may be more important in determining seed survival or further handling (e.g. consumed or recached) by scatterhoarding animals.

Trees of oil tea and many other *Camellia* species are cultivated commercially in large areas across southern China for the cooking oil that is extracted from its seeds (Zhang, 2008). *Camellia* species are also common or even dominant in many subtropical and tropical forests in China (Zhang, 2008). However, until recently there has been little information on how seed predation and seed dispersal by animals affect natural regeneration (Xiao et al., 2003, 2004, 2006, 2013; Chang and Zhang, 2011). Based on our previous and ongoing projects, we have identified that scatter-hoarding rodents (e.g. Edward's long-tailed rat, Pallas's squirrel *Callosciurus erythraeus* and Asian red-cheeked squirrels *Dremomys rufigenis*) are primary seed dispersers for oil tea and several other *Camellia* species in Southwest China (Xiao et al., 2003; Chang and Zhang, 2011; Zhishu Xiao, unpublished data). Therefore, the management and conservation of these scatter-hoarding rodents are important for natural regeneration of *Camellia* species in many disturbed area. Based on this study and Xiao et al. (2013), part of seed crops from a large *Camellia* population can be harvested by local people especially in high-crop years because small seed crops can improve seed dispersal and subsequent survival. In addition, small populations of *Camellia* species may be restored and become common or dominant if scatterhoarding rodents exist in the same area.

In summary, our study presents a testable framework to illustrate how seed size and number interact to predict seed dispersal and survival patterns in animal-dispersed plants. We have shown that the tradeoff between seed size and number manifests at the fruit scale, and both seed size and number have strong but contrasting effects on seed survival and dispersal in oil tea. Moreover, our study also highlights the ecological and evolutionary significances about individual variation of seed size and number in plants and their interactions with biotic and abiotic factors (see Herrera, 2009). In addition, synchronous seed production by oil tea and many other large-seeded plants may also have large impacts on seed dispersal and seedling recruitment of any co-occurring species mediated by numeral and functional responses of both seed predators and dispersers (Moore and Swihart, 2007; Klinger and Rejmánek, 2009; Xiao et al., 2013). Therefore, we expect that consistent with tree- or population-scale seed production, community-level seed abundance may have similar impacts on seed dispersal and seed survival in animal-dispersed plants. Since interspecific and intraspecific variation in seed size and number is common among and within many large-seeded plants as discussed above, the generality of the synthetic framework about size-mediated survival-dispersal patterns presented in this study is worth testing in these plants.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.01.019.

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