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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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A B S T R A C T

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).

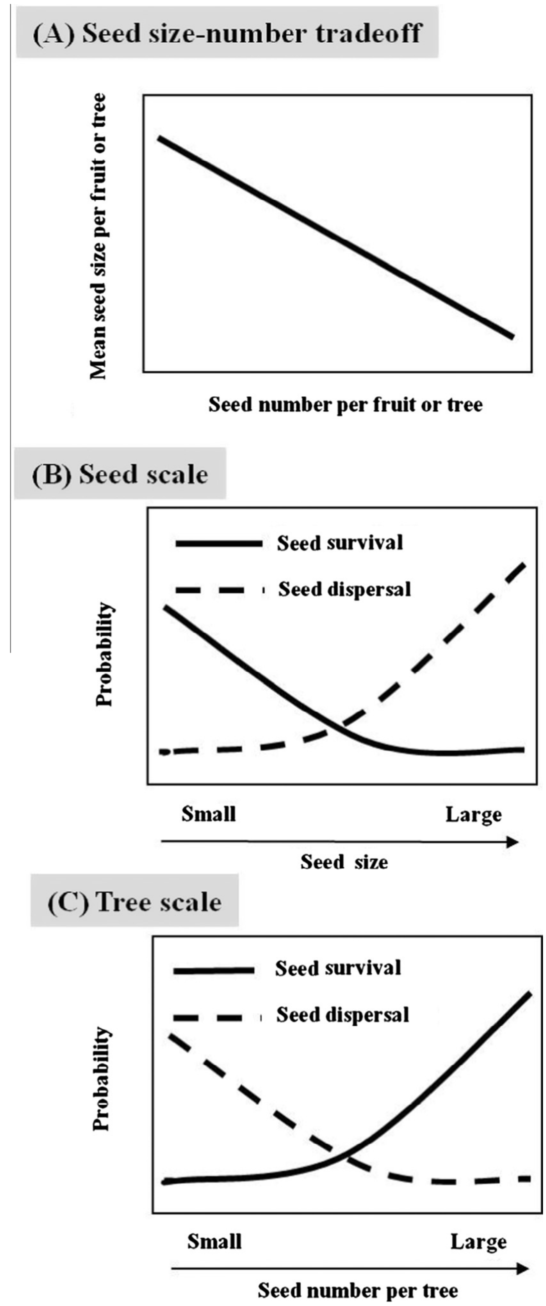

Fig. 1. A testable framework for the seed size-number tradeoff and related predictions on seed survival and dispersal as a function of seed size (seed scale) and seed number (tree scale). (A) Seed size-number tradeoffs predict that seed size and number have a negative relationship at the tree or fruit 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 ⩾ 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