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Poor seed dispersal, seed germination and seedling survival explain why rubber trees (*Hevea brasiliensis*) do not expand into natural forests in Xishuangbanna, southwest China

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ABSTRACT

Studying seed dispersal and the associated processes of germination, seedling establishment and survival are important for understanding plant regeneration dynamics and dispersal ability, especially for introduced plant species. Rubber trees (*Hevea brasiliensis*) have been introduced and cultivated in Xishuangbanna in southwest China for over 60 years. However, almost no adult rubber trees occur in natural forests in the region. In order to determine the factors preventing the expansion of rubber trees into natural forests, we investigated the seed dispersal, seed germination and seedling recruitment of rubber trees. Rubber seeds released in natural forests were frequently visited and largely handled by *Rattus* spp., but the rubber seeds released in rubber plantations were seldom visited or fetched by any animals, indicating that habitat type had a significant effect on the fate of rubber seeds ($P < 0.001$). The majority of released rubber seeds were eaten (57.80% in 2012, $N = 5795$; 64.45% in 2013, $N = 12,455$) and only a very few seeds were cached under forest litter or soil surface (0.32% in 2012 and 0.16% in 2013). When missing seeds (about 30% of all released seeds) were omitted in the analysis, it was found that the majority of the seeds were removed within 10 m (60–90% in different years and different sites), and only few seeds were transported to more than 30 m (maximum distance was 55 m in 2012 and 67 m in 2013). Rubber seeds buried in natural forests had a lower germination rate (mean ± SE = 11.67 ± 2.11%, $N = 300$) compared to those in rubber plantations (mean ± SE = 44.33 ± 4.25%, $N = 300$) (one-way ANOVA, $P < 0.01$). Results from our seed germination experiment and natural regeneration survey showed that rubber seedlings had a very low survival rate, both in natural forests and in rubber plantations. Poor seed dispersal, seed germination and seedling survival may explain why rubber trees do not expand into the natural forests in Xishuangbanna. The findings of this study can help to better understand the natural dispersal ability and regeneration dynamics of rubber trees, providing insights important for forest conservation planning.

1. Introduction

Seed dispersal and the associated processes of germination, seedling establishment and survival are important factors shaping plant regeneration dynamics and dispersal ability (Harper, 1977; Willson and Traveset, 2000; Levine and Murrell, 2003; Almeida and Galetti, 2007). A better understanding of these processes helps to explain plant distribution patterns and predict plant dispersal ranges (Nathan and Muller-Landau, 2000; Muller-Landau et al., 2008). Seed dispersal is a process linking the end of reproductive cycle of adult plants to the establishment of their offspring (Wang and Smith, 2002). Many researchers have made efforts to study the processes of seed dispersal and seedling recruitment (Hamrick and Nason, 1996; Nathan et al., 2000; Dalling et al., 2002; Chen et al., 2014). Animal-mediated seed dispersal has received much attention from researchers, especially in the tropics where more than 90% of tree species rely on animals to disperse their seeds (Howe and Smallwood, 1982; Herrera, 1995). However, the dispersal pattern may vary as plant–animal interactions are often complex and animals often show dissimilar behavior to different seeds and in different environments (Fleming and Estrada, 1993; Muller-Landau et al., 2008; Carlo et al., 2011; McConkey et al., 2012).

Animal-mediated seed dispersal patterns can be influenced by human-induced environmental changes. Anthropogenic introduction of a plant species into a region beyond its native range is an intentional process changing the environments of the species almost completely, which may lead to changes in some of the

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ecological and evolutionary aspects of the species (Myers and Bazely, 2003; Müller-Schärer and Steinger, 2004; Poll et al., 2009; McConkey et al., 2012). The plant seed dispersal syndrome may change with the introduction behavior, because some of the natural dispersal agents may be less abundant or even absent in the new region. This may result in less effective seed dispersal, and further affect the plant regeneration process (Davis, 1989). The varying dispersal performances of plant species in different regions make it difficult to develop generalizable predictions on the dispersal ability and expansion patterns of a species. Therefore, empirical research on the seed dispersal and plant regeneration process of alien plant species remains essential to predict their dispersal ability after being introduced into a new region.

The rubber tree (*Hevea brasiliensis*) is native to rain forests in the Amazon region of South America, including Brazil, Venezuela, Ecuador, Colombia, Peru and Bolivia. Currently, it has been introduced into many tropical or subtropical regions worldwide, and is cultivated in plantations in many of these regions. Rubber trees traditionally grow in low-altitude moist forests, wetlands, riparian zones and forest gaps in environments of high temperature, high moisture and plentiful rainfall (Priyadarshan, 2011). However, in many of the introduced regions, rubber trees are being cultivated in montane areas with non-traditional climatic conditions, and therefore are often threatened by low temperature, drought, strong wind or serious diseases. Compared to the Amazon region, rubber trees in introduced regions may exhibit different phenological and physiological performances. For example, rubber trees are evergreen in the Amazon but deciduous in some introduced regions. Changes in habitat conditions can also affect the seed dispersal patterns of rubber trees. In the rainforests of the Amazon, for example, the ripe rubber seeds often explode into the rivers under the rubber trees, and are carried long distances before they reach new areas suitable for germination (Kubitzki and Ziburski, 1994). In contrast, in many introduced regions there are no rivers to help rubber seeds disperse long distances, and consequently large numbers of seeds simply fall on the ground near mature trees, especially in plantations with high rubber tree density. The rubber seeds in plantations are usually collected for cultivation or to be used as livestock feed, while little attention has been paid to the natural dispersal and regeneration of those rubber seeds so far.

Xishuangbanna in southwest China, located on the north edge of tropics, is a non-native area for rubber trees. In this region, rubber trees have been cultivated for more than 60 years, and rubber plantations have been extensively established, especially in the last two decades. A large proportion of the land used for rubber plantations was reclaimed from natural forests, leading to severe forest reduction and fragmentation (Li et al., 2009). In recent years, many researchers have been increasingly interested in the ecological impacts of rubber plantations on local ecosystems (Wang et al., 2007; Tan et al., 2011; Li et al., 2012), but the natural dispersal and regeneration process of rubber trees remained unnoticed.

Every year, a large number of rubber seeds are produced in rubber plantations, but almost no rubber trees occur in adjacent natural forests. In order to understand the natural regeneration process and reveal why rubber trees do not naturally expand into adjacent natural forests, we investigated the seed dispersal, seed germination and seedling survival of rubber trees. We addressed the following three questions: (1) Are there any animals to fetch rubber seeds that explosively disperse to the ground? (2) Do these animals facilitate the secondary dispersal of rubber seeds? (3) Can rubber seeds germinate successfully and establish seedlings in natural forests into which they are dispersed? By answering these questions, we aimed to understand the seed dispersal and natural regeneration process of rubber trees in the Xishuangbanna region, and determine the factors that are responsible for preventing rubber tree expansion into natural forests.

2. Materials and methods

2.1. Study species

Hevea brasiliensis Müll. Arg. (Euphorbiaceae), commonly called as rubber tree, grows natively in the floodplain forests of the Amazon (Priyadarshan, 2011). Large rubber trees are typically 30–40 m tall, their flowers are monoecious, and the fruits are three-seeded capsules. When the capsules ripen and dehisce explosively, rubber seeds (2.5–3.0 cm long, 3.5–6.0 g in weight) are scattered up to 15 m and may drop into the floodwaters near the mature trees. The fate of these rubber seeds is rarely reported, but there are a few publications (Gottsberger, 1978; Kubitzki and Ziburski, 1994) and some informal sources which provide some information: rubber seeds floating on floodwaters may be eaten by large fish, birds and monkeys, but those animals do not act as dispersers because they digest the seeds; rubber seeds that are not eaten can be carried long distances by the floodwaters and germinate when the floods recede. The trees grow rapidly and favor light, therefore rubber trees are often the first to establish when a gap in the canopy occurs, but they may be shaded out as more trees fill the canopy opening (Priyadarshan, 2011).

The Amazon region provides an ideal environment for rubber tree growth; it has a mean monthly temperature of 25–28 °C and abundant annual rainfall of more than 2000 mm. For rubber tree cultivation, the supporting environment may have 2000–4000 mm rainfall, a mean annual temperature about 28 ± 2 °C and about 2000 h of annual sunshine (Huang, 1981; Priyadarshan, 2011). Rubber seeds are recalcitrant, and can germinate rapidly after ripening but lose viability in a short time even under optimum conditions (about 25 °C, 35% RH) (Roberts, 1973; Husin et al., 1981; Husin, 1990). Low temperatures and high humidity are not optimum for rubber seed germination and seedling emergence. Rubber seedlings are drought- and shade-tolerant to some extent, but require more light during the subsequent regeneration stages (Chen et al., 2010; Yuan et al., 2014).

2.2. Study site description

We conducted our study in Xishuangbanna Prefecture (21°09′–22°36′N, 99°58′–101°50′E), Yunnan province, southwest China. The region has a typical tropical monsoon climate with an annual mean temperature of 22 °C, annual temperature accumulation (the sum of daily temperature means of >10 °C) of 8000 °C, and annual precipitation varying from 1200 to 1556 mm, of which more than 80% falls during the rainy season between May and October (Zhu, 1997). Xishuangbanna has the largest area of tropical rainforest in China and holds rich biodiversity, being a part of the Indo-Burma world biodiversity hotspot (Myers et al., 2000). The rain forests occur mainly in southeastern Xishuangbanna and are distributed in low valleys with altitudes ranging from 480 to 900 m.

We chose two study sites respectively in Menglun (S1: 21°57′09″N, 101°13′34″E) and Mengyang (S2: 22°12′40″N, 100°52′44″E) in the Xishuangbanna National Nature Reserve, and one site in the Nabanhe National Nature Reserve (S3: 22°07′54.43″N, 100°40′16.08″E) (Fig. 1). In the buffer zones of the Nature Reserves, most natural forests once covering the mountains have been cleared up from the bottom up to cultivate rubber trees, with only some small forest patch remaining at the mountaintops. At each study site, we selected a natural forest patch and an adjacent rubber plantation as our study system. The natural forests in S1 and S3 comprise separate forest patches remaining on mountaintops, whereas the natural forest in S2 is located at the downside edge of an intact forest. All three adjacent rubber plantations are at least 15-years old and they produce seeds from August to October each year.