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ECOLOGY

Seed fate of *Castanopsis indica* (Fagaceae) in a subtropical evergreen broadleaved forest

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ABSTRACT. To make comparisons with ecological patterns in temperate forests, we tracked the fates of *Castanopsis indica* seeds from the parent tree through first-year seedling survival in a subtropical forest in Taiwan. We used 320 magnet-inserted seeds and a magnetic locator to examine the post-dispersal pattern and seed fates of *Castanopsis indica* in a 1 ha permanent plot. To identity potential seed predators, we set up four automatic infrared cameras and a video camera in the *C. indica* canopy and on the forest floor. *Macaca cyclopis*, *Petaurista philippensis* and *Callosciurus erythraeus* predated seed in the canopy and *Niviventer coxingi* was a major predator and disperser on the ground. Rodents dispersed seeds only a short distance (mean = 6.8 m ± 4.9 SD). Most of the dispersed seeds were found within 20 m from the experimental stations where they were initially released, and the maximum dispersal distance was 21.6 m. The hoarding depth of all found seeds or seed fragments was ≦ 10 cm, and 54% of the dispersed seeds were found in the top one cm of the litter layer. Almost all of the dispersed seeds (52.8%) were finally eaten by animals, and only one tagged seed successfully established a seedling. These results provide for a clear understanding of the regeneration dynamics of the *C. indica* population at this study site. This study showed that the scatter-hoarding behavior of rodents in the subtropical forest is similar to those in temperate forests.

Keywords: *Castanopsis indica*; Seed dispersal; Seed fate; Subtropical evergreen broadleaved forest.

INTRODUCTION

Seed dispersal has been recognized as a critical process affecting plant regeneration and distribution. Seed dispersal by scatter-hoarding rodents and birds has a significant impact on the natural regeneration of many nut-bearing tree species. Scatter-hoarding behaviors can also have a great influence on seed shadows and on seedling establishment (Vander Wall, 2001; Hulme, 2002). Potential benefits of seed dispersal by scatter-hoarding animals include their introduction into microhabitats suitable for seed survival and their movement away from parent trees to reduce density-dependent mortality. However, rodents act not only as seed dispersers but also as seed predators (Sork, 1984; Miyaki and Kikuzawa, 1988; Sone et al., 2002; Iida, 2006; Takahashi et al., 2006; Gómez et al., 2008). Large-seeded plants suffer heavy pre- and/or post-dispersal seed predation, which may cause important losses in their populations. Determining the ultimate fates of seeds dispersed by animals is important part of ecological and evolutionary studies on plant-animal interactions.

The directed dispersal hypothesis assumes that animals take seeds to nonrandom microhabitats suitable for their establishment and growth (Howe and Smallwood, 1982). Some studies about ant-dispersal have confirmed that directed dispersal is a critical step in the regeneration process (Handel, 1978; Culver and Beattie, 1980; Davidson and Morton, 1981). This is supported by the fact that seeds exposed on the ground surface are prone to damage by heat and desiccation. If the water content of seeds falls below a certain critical level, they lose viability (Gosling, 1989; Finch-Savage, 1992). The benefit of scatter-hoarding is that animals transport the seeds to microhabitats that are favorable for their establishment.

The physical environments and tree traits differ between temperate and subtropical forests. In temperate forests, the seasonal change is quite obvious, with possible snow during the winter and with a nut-ripening period for many deciduous trees in the fall. In subtropical forests, the season change is less obvious, with a nut-ripening period for evergreen trees occurring in the spring. So, the major reason that rodents transport and hoard seeds in the temperate forests is for over-wintering, but in the subtropical forests, it is for later consumption.

Previous studies concerning seed dispersal and predation of Fagaceae species by scatter-hoarding animals were conducted in temperate (Shaw, 1968; Sork, 1984; Kikuzawa, 1988; Janzen and Nielsen, 1986; Stapanian

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and Smith, 1989; Iida, 1996; Sone et al., 2002; Gómez et al., 2003; Iida, 2006; Takahashi et al., 2006; Takahashi et al., 2007; Gómez et al., 2008) or subtropical (Xiao et al., 2004; Xiao et al., 2005; Zhang et al., 2005) regions in China. Seed dispersal and predation of native Fagaceae are rarely studied in Taiwan, although there are about 46 species native to the island.

In the present study, we investigated seed fate of *Castanopsis indica* in a subtropical forest in Taiwan to determine whether scatter-hoarding behaviors of animals in Taiwanese subtropical forests differed from those of temperate forests. *Castanopsis indica* was selected due to its prevalence in subtropical mountainous forests and its spring nut-ripening period. The objective of this study was to link patterns of seed dispersal with those of seedling recruitment, then to follow the fate of pre- and post-dispersal seeds in order to understand the interactions between animals and *C. indica* trees in a subtropical forest. We addressed the following four questions in particular: (1) who are the seed predators and dispersers during the pre- and post-dispersal periods? (2) what are the seed dispersal distance patterns (3) what are the characteristics of the microhabitats where the seeds were dispersed or buried? (4) what are the post-dispersal fates of seeds?

MATERIALS AND METHODS

Study site and study species

We carried out this study from March 2008 to April 2009 in a forest at the Mao-lin Village of Kaoshiung County in southwestern Taiwan (altitude 700-750 m, 22°53' N, 120°44' E). The site lies in the subtropical climate zone, with a mean annual temperature of 20.3°C, and a mean annual precipitation of 3,300 mm. The weather is often cloudy and foggy, with high relative humidity. The habitat is subtropical evergreen broad-leaved forest, which is primarily composed of trees in the Lauraceae and Fagaceae. *Castanopsis indica* (Fagaceae) is a large-seeded evergreen tree, about 20-25 m in height, with a single globose to ellipsoid nut, 1.7-3.2 cm long, 1.4-2.3 cm across, , maturing from March to May, distributed from India to mainland China and Taiwan (Huang, 1996).

Seed predators and dispersers census

To identify potential seed predators in the tree canopy, we set up an iron tower approximately 25 m high at the center of the study plot onto which were installed four automatic infrared cameras during the bur's maturity period. The automatic camera system was composed of an infrared ray sensor connected to a camera. 36-exposure film was used and film was replaced approximately every seven days. Meanwhile, we set up a video camera on the iron tower through the Wireless Sensing Network system to send the video images to the work station's computer. During the seed dispersal experiment, we set up a single automatic infrared camera at each experimental station to identify predators and /or dispersers of tagged seeds on the forest floor. To make a clear and definite identification of the small rodent species, for two consecutive nights during March 2008, 50 trap stations were set at 10 m intervals along each of the five transects and baited with fresh sweet potato and peanut butter. Traps were inspected every morning and the captured rodents were identified and recorded.

Seed dispersal experiment

Fresh seeds were collected from beneath fruiting *C. indica* trees during the bur's maturity period within the study plot in April 2008, and soaked in water to distinguish between well-formed and empty seeds. Three hundred and twenty fresh, intact seeds were selected for the experiment. Each experimental seed was drilled with an electric drill and inserted longitudinally with a small ferrite magnet (diameter, 3 mm; length, 5 mm; weight, 0.3 g), to which a colored plastic tag with a serial number was attached. The mean weight of fresh *C. indica* seeds was 4.03 ± 1.15 g (mean ± S.D., n = 320). After magnet insertion, the seed weight averaged 4.27 ± 1.14 g (mean ± S.D., n = 320), an increase of 0.24 g (6%). These seed tagging methods are widely used for tracking during seed-caching animals' dispersal periods (Iida, 1996; Iida, 2006; Takahashi et al., 2006; Takahashi et al., 2007). The 320 tagged seeds were divided into four groups (80 seeds/group) and randomly distributed at each experimental station (1 m × 1 m). After all released seeds had disappeared, we began searching for them using a magnetic locator (GA-72Cd; Schonstedt Instrument Company, Virginia, USA) across the entire 1 ha study plot. We tracked the magnet-equipped seeds once every other week for the first 3 months, then observed and recorded the emerging seedlings. The definition of seedling we use is "a young plant sporophyte developing out of a plant embryo from a seed." The typical young seedling consists of three main parts: radicle (embryonic root), hypocotyl (embryonic shoot), and cotyledons (seed leaves).

Once we located the position of a ferrite magnet, we carefully retrieved the tagged seeds and determined their fate. Experimental seed fates were classified into 4 categories: (1) eaten *in situ* (seeds were eaten and the magnets remained in the experimental stations); (2) dispersed and eaten (dispersal seeds were buried or not buried and the kernel was eaten); (3) dispersed and intact (dispersal seeds were intact and buried in the microhabitats); and (4) dispersed and missing (dispersal seeds were not found by the magnet and their true fates are unknown)(modified from Li and Zhang, 2003; Takahashi et al., 2006). If the apical portion of the seeds had been damaged, they were considered unviable. We also measured the seed hoard depth and determined seed microhabitats. Post-dispersal seed microhabitats were classified into 6 categories: (1) bare ground (tagged seeds were not buried and scattered on the ground); (2) in the litter layer (tagged seeds were dispersed and buried in the litter); (3) in the fern root system (tagged seeds were dispersed and buried in the fern root system); (4) in the soil layer (tagged seeds were dispersed and buried in the soil); (5) under a fallen tree or branch (tagged seeds were dispersed on the ground and covered by fallen tree or branch); and (6) in a fallen tree hole (tagged seeds were dispersed in the tree hole of a fallen tree) (modified from Li and Zhang, 2003). Furthermore, we measured the distance (straight line) of the tagged seeds or their fragments from the original release stations to the places that they were found. We then reburied the seeds in the cache site, attempting to keep disturbance to a minimum. To determine whether the dispersed seeds were randomly distributed among microhabitat characteristics, seed counts per microhabitat were made and compared to the total cover for that microhabitat using a Chi-square test.

RESULTS

Seed predators and dispersers census

On the iron tower, the four automatic cameras took 144 photographs, including five pictures of Formosan giant flying squirrels (*Petaurista philippensis*), which are olfactorily-oriented nocturnal animals, and three pictures of red-bellied tree squirrels (*Callosciurus erythraeus*). The video camera captured 72 h of video images, including consuming films of Formosan macaques (*Macaca cyclopis*) and red-bellied tree squirrels, which are visually-oriented diurnal animals. Automatic cameras took 140 pictures of rodents at the four seed experimental stations, but the spinous country- and Formosan white-bellied rats' (*Niviventer culturatus*) close resemblance prevented their true identification. Because a spinous country-rat (*Niviventer coxingi*) was trapped during the seed dispersal experiment, we judged the photographed rodents to be the same species. Spinous country-rats played major roles as seed predators and scatter-hoarding seed dispersers in the study site.

Dispersal distance

The dispersal distance of tagged seeds was quite short. Most of the tagged seeds were found within 20 m of the experiment stations from which they were initially released, and the maximum dispersal distance was 21.6 m. A greater proportion (45%) of dispersed seeds or seed fragments was distributed within 5 m (Figure 1). For all found tagged seeds, the median dispersed distance was 6.2 ± 4.9 m (± S.D., mean = 7 m, maximum = 21.6 m, n = 211).

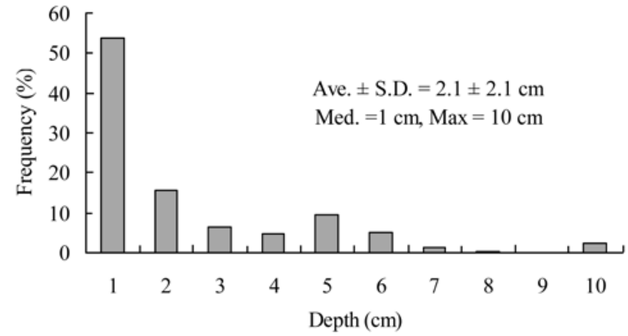

Figure 2. Frequency distribution of the burying depths of 211 hoarded seeds by spinous country-rats (*Niviventer coxingi*).

Microhabitat characteristics

The buried depth distribution of 211 tagged seeds was right-skewed and leptokurtic (Figure 2). A large proportion (54%) of the found seeds or their fragments was found within 1 cm depth. The median depth of buried seeds was 1 ± 2.1 cm (± S.D., mean = 2.1 cm, maximum = 10 cm, n = 211). The frequency distribution of the microhabitat characteristics where the tagged seeds or their fragments were dispersed by the spinous country-rat are shown in Figure 3. The dispersed seeds were not randomly distributed among the different microhabitat characteristics (χ^2=146.2, P<0.001, df=5). A large proportion (60.2%, 127/211) of the buried seeds or seed fragments was distributed in the litter layer. Secondly, 15.6% (33/211) and 13.3% (28/211) of the buried seeds or seed fragments were distributed on bare ground and in the soil layer, respectively. Furthermore, 7.1% (15/211) and 2.8% (6/211) of the buried seeds or their fragments were distributed in the root system or under a fallen tree or branch layer, re-

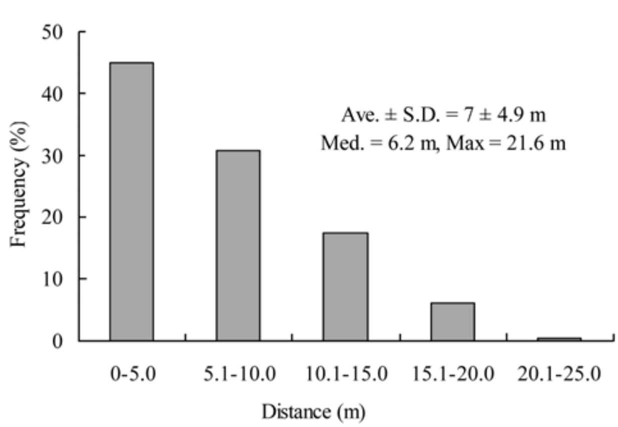

Figure 1. Distance distribution of 211 seeds dispersed by spinous country-rats (*Niviventer coxingi*).

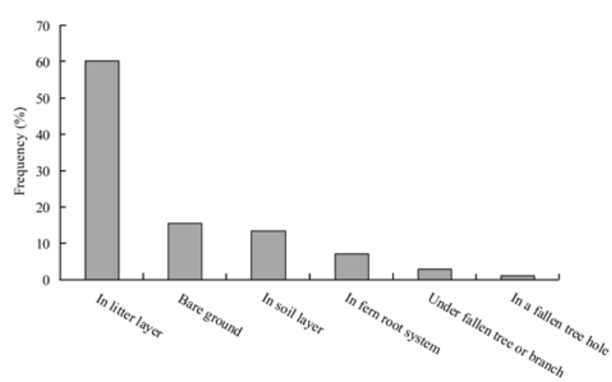

Figure 3. Frequency distribution of the microhabitat characteristics made by spinous country-rats (*Niviventer coxingi*) for 211 hoarded seeds.

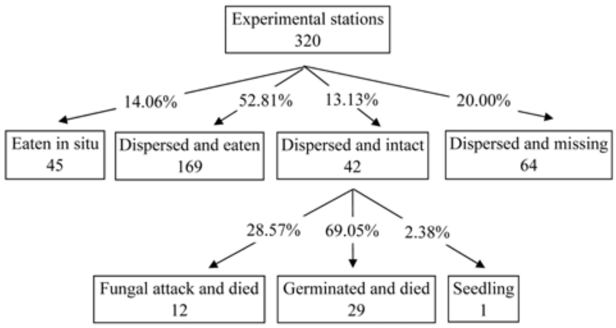

Figure 4. Fate pathway diagram showing the number of initial experimental seeds still alive at each stage, their fates (values inside the boxes), as well as the percentage of seeds moving from one stage, or fate, to the next (values next to the arrows).

spectively. Only 1% (2/211) of the tagged seeds was found in a fallen tree hole.

Post-dispersal seed fates

During the seed dispersal experiment, we relocated most of the dispersed seeds through regular and random searches and determined individual seed fates. The tagged seed fate pathway diagram is shown in Figure 4. Some of the tagged seeds (14.06%, 45/320) were eaten *in situ* (four experimental stations), where they were initially released. Gnawing marks on the seed fragments suggested that the seeds were eaten by rodents. This result indicates that the fates for all seeds *in situ* were "eaten by rodents." All of the tagged seeds, 52.81% (169/320) were dispersed and eaten and 13.13% (42/320) were dispersed and intact. 20% (64/320) of the tagged seeds were dispersed but were not retrieved by the magnetic locator. Among the dispersed and intact seeds, 28.57% (12/42) died from fungal attack, 69.05% (29/42) germinated then died, and only one tagged seed successfully established a seedling.

DISCUSSION

Seed predators and dispersers census

Animals began harvesting a few unripe nuts from the *C. indica* tree canopy in early March, when the burs were still green. According to Vander Wall (2001), the cupules of *Castanea* and *Castanopsis* species are armed with bristly spines that are clearly a mechanism to discourage their harvesting; however, their effectiveness in deterring foragers has not been assessed quantitatively. At maturity, the cupules of these species dehisce, and the nuts appear and then fall to the ground, where nut harvesters have easy access to them. This combination of traits seems to have been designed to protect the nuts during development, when they are attractive and relatively nutritious food items but not yet viable propagules. Therefore, through estimating numbers of empty nutshells below the trees, we found that consumption of *C. indica* nuts peaked from late March through mid-April. The combined effect of these animals' harvesting behaviors appeared to negatively affect the establishment of *C. indica* seedlings. Among these predators, Formosan macaques destroyed the largest quantity of *C. indica* seeds. When the Formosan macaques encountered a fruiting shoot, they usually plucked it and ate the ripest seeds, then threw the remnant to the ground. The video recordings revealed the harvesting manner of Formosan macaques and the original locations of fruiting shoots beneath productive trees. What happens to the fruiting shoot remnants? According to our field observations, these seeds were either consumed or dispersed by rodents or underwent fungal attack, thus losing their ability to germinate.

In the forest ecosystem, rodents are recognized as having an important effect on seed fate (Kikuzawa, 1988; Herrera, 1995; Li and Zhang, 2003; Gómez et al., 2008). During the experimental periods at the four seed experimental stations, all tagged seed visitors were small rodents. Four individual rodents were captured and identified as spinous country-rats. When rodents encountered tagged seeds, they faced two decisions: (1) whether to consume them or not; and (2) if they decided to consume them, whether to eat them *in situ* or carry them to another place (Lima et al., 1985; Lima and Valone, 1986). In the present study, 14.06% (45/320) of seeds were eaten *in situ* and 52.81% (169/320) were dispersed then eaten by spinous country-rats. The purpose for spinous country-rats' hoarding behavior seems for quick seed recovery and consumption rather than for over-wintering. Although the dispersal habits of the rats imposed a high detriment to seeds of *C. indica*, the plants benefited by the survival of some seeds. This result conforms to many of the previous studies (Sork, 1984; Miyaki and Kikuzawa, 1988; Herrera, 1995) on temperate forests.

Dispersal distance

Seeds were not dispered very far; in fact, most samples were found within 20 m of the experimental stations from which they were initially released. The maximum and mean dispersal distances of *C. indica* were 21.6 m and 6.8 m, respectively, which is in agreement with many previous reports for temperate forests (Sone et al., 2002; Li and Zhang, 2003; Iida, 2006). However, all the retrieved tagged seeds were within the 1 ha permanent plot. This implies that the dispersed tagged seeds could not help *C. indica* extend its population. Although the spinous country-rats appear to be the only dispersers at the study site, they are moderately effective locally.

Microhabitat characteristics

The majority of seeds or their fragments (54%) found at the study site were located within 1 cm of the ground's surface. The condition of this microhabitat seems more conducive to rodents' seed recovery than to their seed consumption. Although some spinous country-rats buried seeds in the deeper soil (10 cm), where seed survival and germination probability increased, it inhibited the establishment of seedlings because of the greater distance the seed shoots required to reach the surface. The spinous country-rats buried most *C. indica* seeds in the favorable microhabitat (litter layer), but few seeds germinated and produced seedlings, resulting in a low germination rate. The main reason for the buried seeds' low survival rate was their high rate of recovery and consumption by spinous country-rats, which was also reported for the temperate forests (Sone and Kohno,1999; Sone et al.,2002). These results suggest that *C. indica* seeds clearly benefit from transportation and burial in the litter layer by spinous country-rats, but that these benefits are usually negated by the very high rate of seed recovery.

Post-dispersal seed fates

Although nearly all of the seeds were destroyed by rodents, a small number of them managed to escape animal predation and establish seedlings (Herrera, 1995; Hulme, 2002; Li and Zhang, 2003; Forget and Wenndy, 2005) in the temperate forests. In this study, almost all of the tagged seeds were eaten *in situ* or dispersed and eaten by spinous country-rats. Among the seeds dispersed and cached by the rats, only 1 tagged seed germinated, survived and established a seedling during the first season in 2008. There are 5 major reasons why seeds dispersed and buried by the spinous country-rats subsequently lost their germination abilities: (1) most of the buried seeds were retrieved and eaten by the rodents; (2) the hole through which the small ferrite magnet was inserted may have facilitated fungal attack of tagged seeds; (3) the hole may have allowed too much water to permeate tagged seeds; (4) seeds were disturbed and damaged by the authors during cache inspection and reburial; and (5) germinated seed shoots were unable to penetrate the thick soil layer. Twenty percent (64/320) of the dispersed seeds were not retrieved by the magnetic locators, so we could neither understand the cause of their disappearance nor their post-dispersal fates.

Castanopsis indica seeds can germinate quickly once they fall to the ground if temperatures and moisture levels are moderate. The spring rain season at the study site occurs from March to May and *C. indica* nut-ripening periods are from March to June, so the spinous country-rats attempted to quickly recover buried seeds after scatter-hoarding. In contrast, the buried seeds quickly attempted to germinate and establish seedlings before they could be recovered and consumed by spinous country-rats. Thus, there was competition between spinous country-rats and buried seeds.

This study shows some traits of interaction between seed-dispersing rodents and *C. indica* trees. First, spinous country-rats dispersed the seeds near the experimental stations. Second, the depth and microhabitat of most seeds buried by spinous country-rats was within 1 cm and in the litter layer, respectively. These traits are apt to help the spinous country-rats retrieve dispersed/buried seeds, resulting in their near total consumption by rodents. In fact, only 1 tagged seed successfully established a seedling. The results show that the scatter-hoarding behaviors of rodents in the subtropical forests are similar to those in the temperate forests.

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一個亞熱帶常綠闊葉林印度苦櫧（殼斗科）種子的命運

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我們在一個 1 公頃的永久樣區內執行一個種子散播實驗，將 320 粒的印度苦櫧 (*Castanopsis indica*) 種子植入磁鐵，使用金屬探測器來檢視種子散播後的分布模式，並追蹤種子的命運及幼苗建立的情形。為了記錄取食種子的動物，我們分別在印度苦櫧的樹冠層及地被層設置 4 個紅外線自動照相機及一組無線網路攝影機，台灣獼猴 (*Macaca cyclopis*)、大赤鼯鼠 (*Petaurista philippensis*) 和赤腹松鼠 (*Callosciurus erythraeus*) 是樹冠層主要的種子取食者；刺鼠 (*Niviventer coxingi*) 則是地被層主要的種子取食者。大部分被刺鼠散播的種子距離都在 20 公尺內，平均距離是 6.8 公尺，最遠的距離是 21.6 公尺。所有被偵測到的種子或種子碎片有 54% 被儲藏在深度 1 公分的腐植層中。大部分被散播的種子命運都是被動物吃掉，僅有一粒被上標的種子成功建立幼苗。此研究結果提供我們清楚地了解此研究地區印度苦櫧的更新動態，且顯示老鼠散播儲藏的行為相似於一些溫帶森林。

關鍵詞：印度苦櫧；種子散播；種子命運；亞熱帶常綠闊葉林。