RESEARCH ARTICLE
doi: 10.2306/scienceasia1513-1874.2008.34.129

Seed dispersal and seedling recruitment in the light-demanding tree *Choerospondias axillaris* in old-growth forest in Thailand

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Received 7 Nov 2007
Accepted 18 Jan 2008

ABSTRACT: As seeds are the only movable stage in the plant life-cycle, their dispersal determines the chances of recruitment and survival away from the parent trees and the distribution of the next generation. We studied the light-demanding tree, *Choerospondias axillaris* (Anacardiaceae), whose pyrenes ("seeds") are dispersed mainly by deer and gibbons, to determine if seed dispersal is random with respect to parent trees and preferred germination and recruitment sites. Research was carried out during 2004 and 2005 on the Mo Singto 30-ha forest dynamics plot, Khao Yai National Park, in which all trees down to 1 cm in diameter are mapped and measured. The species has a relatively large number of adults but very few juveniles 1–10 cm in diameter and appears not to be replacing itself in this old-growth forest. Dispersal into gaps is essential for recruitment, but gaps make up less than 10% of the area. Dispersal by sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), and gibbons (*Hylobates lar*) is almost random over the plot and not directed to gaps. In the 2 years of the study, less than 1% of seeds found in sub-quadrat samples were in gaps, but in the following year, approximately half of 1-year old seedlings were found in gaps. While 4.5% of the 750 sub-quadrats contained seedlings, the percentage of sub-quadrats in gaps containing seedlings was 11% and 23% in the 2 years of census. Only seedlings in gaps survived to the second year. In this population, recruitment is limited by a shortage of gaps in which seedlings can grow. Both the size distribution of adults and the dependence of seedling recruitment on light in gaps suggest that this tree population may depend on episodic forest disturbances large enough to create much larger gaps in order to maintain itself. If so, this species cannot maintain itself in mature forest and may be in perpetual disequilibrium.

KEYWORDS: deer, gap, seed dispersal, spatial pattern, seedling recruitment, tropical tree, Anacardiaceae

INTRODUCTION

Seed dispersal is an essential process in the life cycle of plants that determines patterns of migration and colonization, and whether seeds can germinate and survive to produce the next generation. Numerous dispersal mechanisms have been found in plants throughout the world[1]. In general, the advantages of seed dispersal are to escape unsuitable conditions near the parent trees (escape hypothesis), and to colonize vacant habitats or suitable micro-sites for recruitment (directed seed dispersal, or seed dispersal biased toward favourable sites)[2–5]. Seed dispersal helps to avoid the density- and distance-related mortality caused by specialized seed predators and herbivores near the parent trees[6,7]. Growing evidence, mostly from neo-tropical trees, validates this idea[8,9], although not all species conform to it[10]. In tropical forest, seed dispersal of light-demanding trees into gaps has been highlighted as an example of directed seed dispersal[11]. For instance, bellbirds disperse more than a half of all seeds into tree-fall gaps[12]. Most evidence about directed seed dispersal comes from bird-dispersed trees; there is relatively little information about mammal-dispersed species, which are important in tropical Asia[13].

Spatial analysis, explicit as well as implicit, is crucial to the understanding of the role of seed dispersal as it helps to determine the dispersion and location of the next generation[14,15]. Animal behaviours are particularly difficult to model because they have complex movement patterns which are not easily predicted[14]. Several studies have demonstrated effects of movement pattern on the spatial pattern of seeds[16–18]. Most studies of animal dispersal in the tropics have focused on birds[18–20], relatively few have dealt with mammals, which are more restricted in their movement.

In this study, we investigated dispersal of seeds of a light-demanding tree in seemingly mature evergreen forest, whose seeds are swallowed and dispersed primarily by gibbons and two species of deer. We investigated where these mammals drop seeds in relation to parent trees as well as gaps, and how this affects recruitment and survival of seedlings. We also wished to determine the importance of gaps in the forest to recruitment, and whether the incidence of gaps plays a role in recruitment limitation.

We addressed the following questions in particular: (1) Can deer or gibbons disperse seeds directly into gaps? (2) What is the dispersion pattern of seeds and seedlings of *C. axillaris*? (3) How did gap dynamics in the two years of the study influence seedling recruitment?

MATERIALS AND METHODS

Study sites

This study was carried out on the Mo Singto forest dynamics plot, located in seasonal evergreen forest in Khao Yai National Park, central Thailand (101° 22' E and 14° 26' N, 725 to 815 m in altitude). The first census of trees larger than 10 cm in diameter at breast height (dbh) was completed in 2001, and a second census completed in 2005 included all trees down to 1 cm dbh. The main habitat appears to be primary forest that has never been cleared by humans, but a patch of secondary forest about 20 years old borders the plot on the northern side. The average annual rainfall is 2,200 mm, mostly between April and October. Minimum and maximum monthly average temperatures are about 19 °C and 28 °C, respectively.

Study species

Choerospondias axillaris (Roxb.) Burtt & Hill (Anacardiaceae) is a common species of the main canopy reaching about 30 m in height. It is an important species for forest restoration with high seedling survival in open areas[21]. Its distribution ranges from Nepal, China, Japan through Indo-China[22]. It flowers January to March, and sets fruit April to June. Fruits are ellipsoidal and ca. 30×21 mm in size with a thin skin covering succulent, fibrous pulp clinging to 5-chamber, capsule-like pyrenes approximately 21×16 mm in size (hereafter usually referred to as "seeds" for simplicity). Fruit usually begins ripening in July and by the end of November there is no more fruit on the trees (unpublished data). Although each pyrene contains 5 embryos, only one usually germinates and survives as a seedling. The pyrenes are dispersed by mammals, the most significant of which are two species of deer, sambar (*Cervus unicolor*) and muntjac (*Muntiacus muntjak*), and gibbons (*Hylobates lar*)[23]. In China, muntjac is the most important dispersal agent of the species[24]. The recruitment of seedlings may occur from seeds dropped within the past 6 months because the length of dormancy varies from 15 days to at least 200 days[21].

Seed and seedling census

To census seeds and seedlings, we surveyed a central 2×8 m sub-quadrat in each of the 750 20×20 m quadrats on the plot. All *C. axillaris* seedlings found were measured and mapped. Generally, seeds deposited by deer were regurgitated in piles. The position of the centre of each pile and the number of seeds it contained were recorded. The sub-quadrat was considered to be in a gap if at least 80% of the canopy above 5-m was open.

The censuses were carried out from November 24 to December 21 in 2004 and from November 30 to December 9 in 2005. Fruiting trees were checked each year by searching for new fruits under the tree crowns during late October and early November, the period when most trees have ripe fruit.

Distance of seeds and seedlings from fruiting trees

The distance of seeds and seedlings to the nearest fruiting trees was studied using the data from the sub-quadrat census. Since seeds or seedlings that are near the edge of the plot could have been dispersed from trees outside the plot, we considered only quadrats that were at least 100 m from the edge of the plot for this part of the study. We also compared the distribution of distances with the distribution obtained from a simulated random placement of the same number of seeds and seedlings in the sub-quadrats. The random placement was repeated 1,000 times to obtain an average and standard deviation for comparison with the distribution of the measured data.

Statistical analysis

A comparison of the numbers of seeds in sub-quadrats in 2004 and 2005 was carried out using the non-parametric Wilcoxon signed rank test because the distribution was highly skewed, and most sub-quadrats had no seeds or seedlings. The association of sub-quadrats which had seeds or seedlings in 2004 with those in 2005 was tested using the chi-squared test. The correlation between gaps and sub-quadrats with seedlings was also analysed with the chi-squared test.

To study the spatial pattern of gaps, seeds, seedlings and fruiting trees, the plot was divided into 1-ha squares (5×5 quadrats). The frequencies analysed were the numbers of sub-quadrats per 1-ha area that were positive for gaps, seeds, seedlings, or trees. The expected values were generated using the Poisson distribution with the same mean. Classes with expected values less than 5 were pooled with adjacent classes. Finally, the chi-squared test was applied to determine the goodness-of-fit[25]. This method was also applied to compare the distance from the nearest fruiting trees of the actual to the simulated data of the seeds and seedlings. The distance categories were lumped into 3 groups: (1) < 30 m; (2) 30–59 m; and (3) ≥ 60 m from the tree trunk.

RESULTS

Trees and forest gaps

During 2004–2005, there were approximately 160 trees (dbh ≥ 10 cm) and 6 saplings (dbh 1–9.9 cm). The species is dioecious, and the number of trees producing fruit in the years 2003, 2004, and 2005, was 68, 46, and 40, respectively. Seedlings in a given year may have developed from seeds produced in that year or in the previous year. The spatial distribution of fruiting trees at the 1-ha scale strongly deviated from randomness for the fruiting trees of 2003 and 2004 ($\chi^2 = 7.93$, df = 3, $P < 0.001$) and those of 2004 and 2005 ($\chi^2 = 40.4$, df = 2, $P < 0.01$) (Figs.1 and 2).

The percentage of gap area on the plot was 9.3% (70 out of 750 sub-quadrats) in 2004 and 6.4% (48 out of 750 sub-quadrats) in 2005. However, 25.7% (18 out of 70 sub-quadrats) of forest gaps in 2004 still had not been covered by tree canopy in 2005, implying that the recovery rate of the canopy was about 74% of gaps per year. In other words, approximately 37% (18 out of 48 sub-quadrats) of the gaps in 2005 were from gaps in 2004.

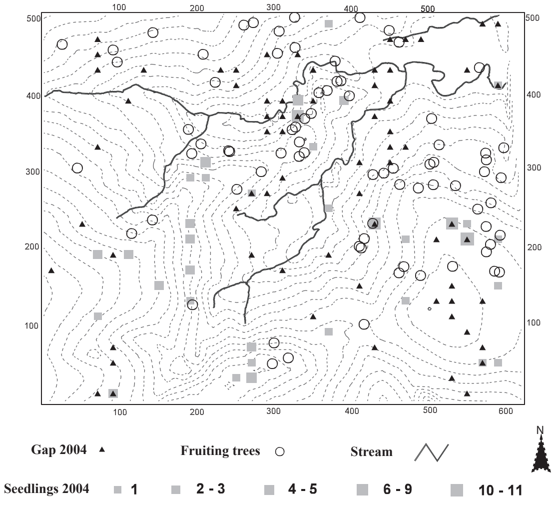

Fig. 1 Map of seedlings in 2004, the fruiting trees of 2003 and 2004 (open circles), sub-quadrats with gaps (triangles) and sub-quadrats with seedlings (squares).

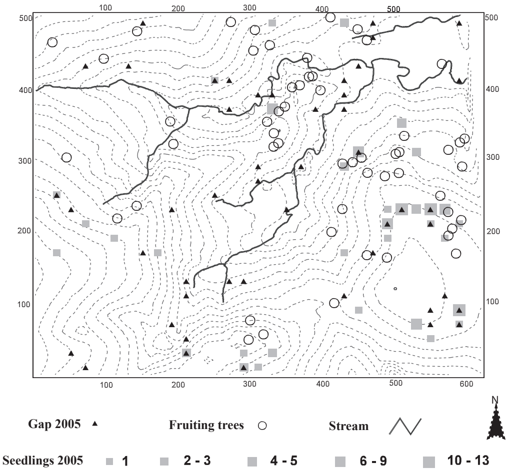

Fig. 2 Map of seedlings in 2005, the fruiting trees of 2004 and 2005 (open circles), sub-quadrats with gaps (triangles) and sub-quadrats with seedlings (squares).

At the 1-ha scale, the data showed that the distribution of gaps in 2004 was clustered, whereas in 2005 the distribution did not show any statistically significant patterns (2004: $\chi^2 = 8.169$, df = 3, $P < 0.05$; and 2005: $\chi^2 = 1.661$, df = 2, $P > 0.05$).

Seeds

The total number of seeds found in all the sub-quadrats was 1,747 in 2004 and 495 in 2005. The number of seeds in sub-quadrats differed between years (Wilcoxon signed rank test: $Z = 3.986$; $n = 750$; $P < 0.001$). The estimated number of seeds in the whole 30-ha plot for the 2 years was 44,925 and 12,375.

Although the number of seeds on the whole plot differed between years, the percentage of sub-quadrats containing seeds was nearly the same in both years, 4.9% (37 out of 750 sub-quadrats) in 2004 and 4.8% (36 out of 750 sub-quadrats) in 2005. The main difference between years was in average pile size which was 47.2 in 2004 and 13.8 in 2005 (Fig. 3). The presence or absence of seeds in sub-quadrats in 2005 did not correlate with that of seeds in 2004 ($\chi^2 = 0.93$, df = 1, $P > 0.05$).

The percentage of sub-quadrats with deer-dispersed seeds was 2.5% (19 out of 750 sub-quadrats) in 2004 and 1.7% (13 out of 750 sub-quadrats) in 2005. Deer-dispersed seeds were found mostly in the middle-west area of the plot (Figs. 4 and 5). At the

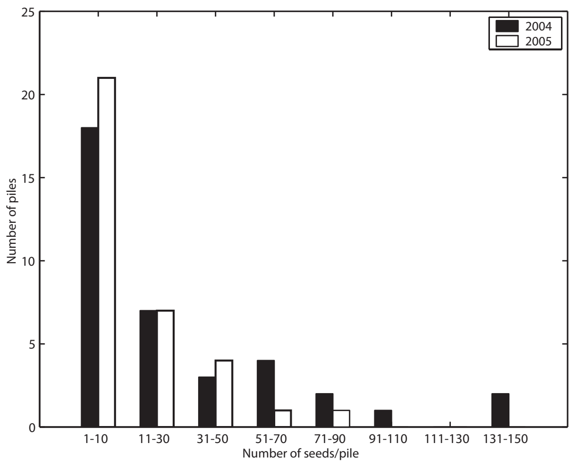

Fig. 3 Frequency distribution of seed piles into size classes. The largest pile (750 seeds) is omitted in 2004 because it is an extreme outlier, and sub-quadrats 3,217 and 4,117 in 2005 are omitted because the seeds were not evidently dropped by gibbons and deer.

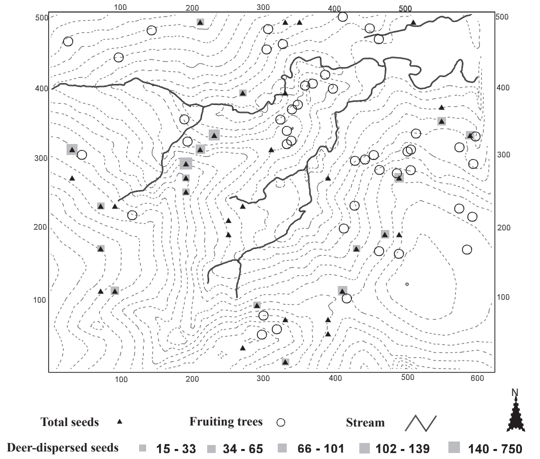

Fig. 4 Map of seeds in 2004, fruiting trees of 2004 (open circles), sub-quadrats with seeds (triangles) and sub-quadrats with seedlings (squares).

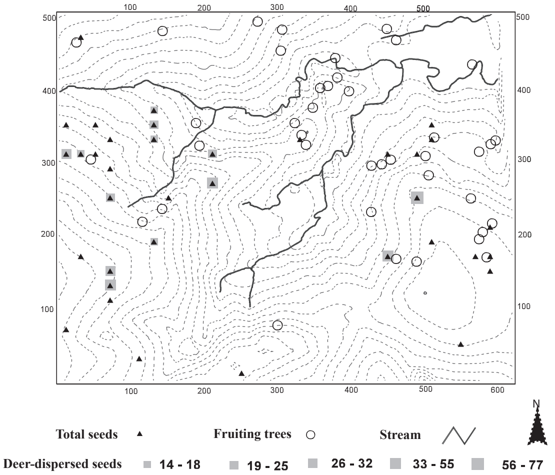

Fig. 5 Map of seeds in 2005, fruiting tress of 2005 (open circles), sub-quadrats with seeds (triangles) and sub-quadrats with seedlings (squares).

1-ha scale, the sub-quadrats with deer-dispersed seeds appeared to be distributed randomly in both 2004 ($\chi^2 = 2.728$, df = 1, $P > 0.05$) and 2005 ($\chi^2 = 1.209$, df = 1, $P > 0.05$). However, in both cases the tests are not totally conclusive in indicating randomness as there are too few data to obtain expected values of more than 5 sub-quadrats containing seeds.

Seeds dispersed by gibbons were dropped singly or in small loose clusters of less than 10 seeds, whereas those dispersed by deer were regurgitated in larger piles containing between 14 and 140 seeds, with the exception of one pile which was found to contain 750 seeds. It cannot be proven that all seeds in small clusters were dropped by gibbons, but no other animal is known to systematically consume *C. axillaris* and drop these singly or in small clusters. Muntjac tended to deposit seeds in smaller piles (of usually less than 100) than sambar. The number of large piles (> 100 seeds) was greater in 2004 than in 2005, suggesting that in 2005 muntjac were more abundant or ate more of the fruit than sambar. The number of seeds in piles < 10 was 36 (2% of total) in 2004 and 80 (17% of total) in 2005. Hence, deer dispersed 98% of all seeds in 2004 and 83% in 2005, but gibbon-dispersed seeds appeared in 2.4% (18/750) of the sub-quadrats in 2004 and 3.1% (23/750) in 2005. It is likely that gibbon-dispersed seeds were underestimated because single seeds or small clusters are much easier to overlook than piles of deer-dispersed seeds.

Seeds of *C. axillaris* were dispersed as far as 70 m (Fig. 6). However, the dispersal distance was mostly between 10 and 40 m from fruiting trees in both years. The actual data differed from randomness at large distances (> 90 m) in both years, and at short distance (< 10 m) in 2005. The distribution of the actual data differed significantly from a random distribution in having a smaller than expected mean than the simulated data in both 2004 ($\chi^2 = 6.666$, df = 1, $P < 0.05$) and in 2005 ($\chi^2 = 26.261$, df = 1, $P < 0.001$).

For seeds dispersed into gaps, it was found that only 2.7% of sub-quadrats with gap (1 out of 37 gap) in 2004 and 2.1% (1 out of 48 gap sub-quadrats) in 2005 contained seeds. The numbers of seeds found in the sub-quadrats with gaps was < 0.1% (1/1797) in 2004 and 0.4% (2/495) in 2005. None of the seeds found in gaps were dispersed by deer. Gibbons could disperse seeds from the edge of gaps, especially as seeds dropped from tall trees are often deflected by

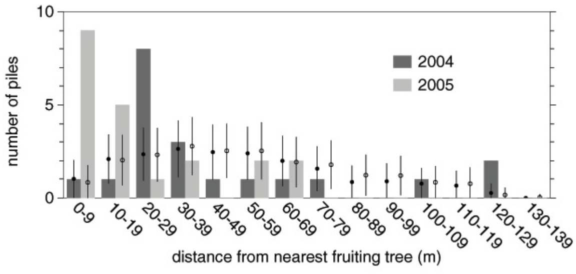

Fig. 6 Distance of sub-quadrats with seeds from the nearest fruiting trees in the same year compared with the simulated random distribution (dots with standard deviation shown by vertical lines).

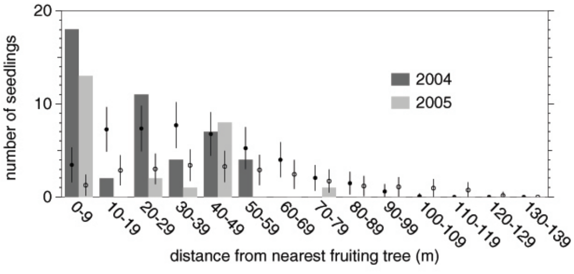

Fig. 7 Distance of seedlings from the nearest fruiting trees in the same year compared with the simulated random distribution (dots with standard deviation shown by vertical lines).

branches and foliage.

Seedlings

A total of 88 seedlings was found in the sub-quadrats in 2004 and 112 seedlings in 2005. The number of seedlings found per sub-quadrat did not differ significantly between years (Wilcoxon signed rank test: $Z = 0.659$; $n = 750$; $P > 0.05$). The estimated number of seedlings on the 30-ha plot was 2,200 in 2004 and 2,800 in 2005. The percentage of sub-quadrats where seedlings were found was nearly the same in both years, 4.6% (35 out of 750 sub-quadrats) in 2004 and 4.5% (34 out of 750 sub-quadrats) in 2005. Furthermore, the presence of seedlings in sub-quadrats in 2005 was correlated with presence or absence in 2004 ($\chi^2=13.49$, df=1, $P<0.001$).

Gap sub-quadrats tended to contain more seedlings than non-gap sub-quadrats: 11 % (8/70) of gap sub-quadrats contained seedlings in 2004, and 23 % (11/48) in 2005. Nearly half of all seedlings were found to be in gaps: 45% in 2004 and 51% in 2005. The recruitment of seedlings in sub-quadrats was strongly correlated with gaps both in 2004 ($\chi^2 = 7.93$, df = 1, $P < 0.005$) and in 2005 ($\chi^2 = 40.4$, df = 1, $P < 0.0001$).

The sub-quadrats with seedlings in 2004 and 2005 seemed to be aggregated, especially in areas with more numerous gaps (Figs. 1 and 2), but the spatial pattern at the 1-ha scale did not differ from a random distribution in either 2004 ($\chi^2 = 2.262$, df = 1, $P > 0.05$) or 2005 ($\chi^2 = 1.966$, df = 1, $P > 0.05$). The survival of seeds was very low, only 0.2% (3/1747) of seeds in 2004 developed into seedlings. The survival of seedlings from 2004 to 2005 was 4.5% (4/88 seedlings). All of these were in a single sub-quadrat in a gap.

In both years, most seedlings were less than 10 m from the nearest fruiting tree, although they were found as far as 80 m away (Fig. 7). This distribution was significantly different from a random distribution in having a smaller than expected mean than the simulated data in both 2004 ($\chi^2 = 18.594$, df = 1, $P < 0.001$) and in 2005 ($\chi^2 = 15.081$, df = 1, $P < 0.001$).

DISCUSSION

This study supports earlier observations that *C. axillaris* is a light-demanding species[21]. Nevertheless, nearly half of all seedlings were found in non-gap areas, which usually receive less light. However, we did not measure the quality of gaps or light intensity. In some gaps, there was no light available below 2 m from the ground due to the presence of invasive weeds or lianas covering a fallen tree. The quality of these gaps may improve in the following year after these weeds or woody climbers die, allowing *C. axillaris* to recruit. Direct measurement of light intensity may result in improvement of the correlation between gaps and seedling recruitment.

It is clear that deer do not disperse seeds into gaps, and the tangle of fallen trees and lianas probably prevents deer from entering many gaps. Deer tend to bed down in areas from which they can rapidly flee from an approaching predator.

Seed dormancy is a kind of storage effect which may be an adaptation for avoiding competitive exclusion[26]. If a seed is not dispersed into part of a gap, it might be possible for the seed to lay dormant until the area becomes a gap. Moreover, the dormancy period of *C. axillaris* is variable[21], which might be another strategy of *C. axillaris* to obtain an advantage in an unpredictable environment.

Recruitment limitation was also found in *C. axillaris*, but unlike most species on the Barro Colorado plot[27,28], it was not at the dispersal stage. The recruitment limitation of *C. axillaris* occurs at the growing stage of the seedling, as seedling mortality occurs mostly in the second year. If the canopy recovery rate is high, the availability of light may still limit the seedlings growth.

The distribution of piles of seeds was rather random in both years, and it was not greatly influenced by the distribution of trees. This implies that the deer usually regurgitated seeds at some distance from where they were eaten. The advantage of random dispersal is that the spatial pattern of gaps changes unpredictably from one year to the next. If a seed does not land in a gap, as the seeds have a dormancy period, there is still a chance that the seed will germinate later if the area becomes a gap.

Deer are capable of longer distance dispersal than was recorded in this study. Long-distance dispersal is dispersal to a greater distance than normal and is important for the invasion and colonization in many plant species[29,30]. Since *C. axillaris* has a very low recruitment rate in primary forest, we hypothesize that long-distance dispersal is probably needed for sustaining the population in a changing landscape. The white-tailed deer, for example, is able to disperse seeds a long distance to suitable habitat[31] for herbs in North America. In Khao Yai, muntjac and sambar are able to forage across several habitats and may carry seeds from the forest. Longer distance dispersal would be possible if, for example, deer have to run away from predators while having seeds in their gut. We occasionally found seed piles in grassland < 1 km from the plot. Moreover, recent studies using molecular techniques have demonstrated that long distance dispersal in tropical trees may be more common than we have thought[32] and lead to multiple scales in the dispersal distribution[33]. The role of long distance dispersal of *C. axillaris* is a potentially important topic for further study.

The main conclusions of this study are: (1) dispersal of *C. axillaris* seed piles by deer, and smaller numbers by gibbons, is more or less random and not directed toward optimal recruitment sites, at least within the forest; (2) although seeds do germinate in the forest, seedling growth requires high light conditions; and (3) there are insufficient gaps in the mature forest to allow recruitment of juveniles. Indeed, the tree population at the Mo Singto plot appears to be in disequilibrium and it may be dying out. We are forced to conclude that the population requires disturbance on larger spatial or temporal scales to maintain itself. Hence, we are faced with a multiple scales problem[34,35] requiring a longer time scale (slow scale), and perhaps a broader spatial scale at the landscape level, across which longer deer movements may be important to sustain the population. Smaller scale dispersal by either deer or gibbons, coupled with episodic disturbance on a longer time scale, could provide for the recruitment of this species in the forest. Theoretical as well as empirical study will be needed to investigate the population dynamics at wider spatiotemporal scales.

ACKNOWLEDGEMENTS

The travel grant for this research was supported by Department of Biology, Mahidol University. We are grateful to the Department of Parks, Wildlife and Plant Conservation for permission to conduct this research. We thank Chatchai Chainontee and others who helped us tirelessly in the field, and Michael A. Allen for helping with figures and providing advice and comments on the manuscript.

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