SEEDLING MORTALITY OF SIX PHILIPPINE RAIN FOREST TREE SPECIES: A TEST OF THE 'ESCAPE HYPOTHESIS'[1]

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Abstract. This study tests Janzen's escape hypothesis (1970, see also Connell 1971), suggesting that survival chances of forest tree propagules increase upon escape from their parents' vicinity, where the probability of being attacked by parasites of the parent tree or being eaten by seed predators searching near the parent tree is much higher. In this study the survival of propagules of six animal-dispersed tree species of a lowland rain forest on Panay, Philippines, was assessed as a function of dispersal distance from the parent tree. Dispersal distance was experimentally manipulated from 0 m to 100 m while keeping density of propagules constant. Survival of seeds and seedlings was recorded at weekly intervals during 14–26 weeks. The six individual study trees belonged to six species: *Microcos stylocarpa* (Tiliaceae), *Neoscortechinia philippinensis* (Euphorbiaceae), *Syzygium* sp. (Myrtaceae), *Platea excelsa* var. *borneensis* (Icacinaceae), *Ficus* sp. (Moraceae), *Pygeum vulgare* (Rosaceae). The results obtained for four of the six species support the hypothesis of an advantage through increasing dispersal distance from the parent tree, thus falsifying the idea of density-dependence as a necessary cause. For one species, dispersal away from the parent did not result in higher survival, and for another survival rate of seeds beneath the crown of the parent tree was higher than farther away. For one species we found survival chances of bare seeds to be significantly higher than of fruits. The causes of mortality varied between species and dispersal distances. Nearly all seeds of *P. excelsa* laid out under the crown were eaten by rodents, whereas most of the fast-growing seedlings of *N. philippinensis* died from pathogens at later stages. Over half of the *Syzygium* sp. fruits and seeds disappeared for unknown reasons within the first two weeks and *M. stylocarpa* individuals died for various reasons. *Ficus* sp. seeds suffered heavily from being eaten and/or carried away by ants within the first two weeks. Seed mortality in *P. vulgare* occurred through insect rather than small mammal frass or attack by pathogens. The almost complete mortality of propagules under the parent tree may have far-reaching community effects in opening up space for other, perhaps rare species, thus increasing species diversity. *Accepted 14 January 2003.*

Key words: Community ecology, density-independent mortality, dispersal, dispersal pattern, escape hypothesis, Philippines, seed, seedling survival.

INTRODUCTION

Based on his observations on South American rain forest trees, Janzen (1970) suggested the 'escape hypothesis' to account for their dispersal pattern. He assumed that the spatial distribution of scatter-dispersed tree species was a reflection of their dispersal system and seedling mortality after dispersal.

The likelihood of a seed becoming established at a site is not proportional to the number of seeds arriving there. For example, only few seeds survive under the parent tree despite the fact that many fruits fall there (Connell 1971, Schupp 1988, Howe 1993). To account for this observation various mechanisms have been invoked. Furthermore, to avoid competition for nutrients and space some plants produce chemicals (allelopathics) that prevent propagules from establishing in the vicinity of the parent. In other cases, parasites of the mother tree harm seeds and seedlings which may lead to their death (Wilson & Janzen 1972, Webb & Willson 1985). This includes damage to leaves caused by beetles and other herbivores and infestation with pathogens. Augspurger (1984) showed that the probability of a disease killing seedlings declines with increasing dispersal distance, decreasing seedling density, or increasing light and associated microclimatic factors in treefall gaps. By contrast, Terborgh *et al.* (1993) found no distance effect when mammal seed predators searched the

ground around the parent trees thoroughly. Clark and Clark (1984) identified density as the salient and necessary variable bringing about the distance-related mortality expected in the Janzen-Connell model. This unnecessarily restricted portrayal of the model persevered until the present day (Wang & Smith 2002). The present study will show this view to be not universally valid.

It was the primary intention of this study to test the hypothesis underlying the Janzen-Connell model, whether the chance of a propagule to survive under the parent tree is lower than farther away. Propagule density was kept constant so that distance was the only variable affecting survival. Six different Philippine rain forest species were chosen for this study. All of them appeared to be spatially dispersed, i.e., not visibly clumped around parent trees, a prerequisite for testing the 'escape hypothesis'.

MATERIALS AND METHODS

Study site. The experiments were carried out on the island of Panay, Philippines, from July 1997 until January 1998 and from March until July 2001 (*Ficus* sp., *Pygeum*) near the research station of the Philippine Endemic Species Conservation Project at Sibaliw, municipality of Buruanga (11°49.188'N, 121°58.064'E). The experiments were conducted in a relatively undisturbed mature forest on the NW Panay peninsula at an elevation of 400–500 m a.s.l. Intensive weather data were gathered through a period of 30 months between the years 1998 and 2001. The rainy season generally lasted from June until January. The average monthly maximum temperature fluctuated between 24.0°C (February 1999) and 27.6°C (October 1998), as did the average monthly minimum temperature between 20.5°C (January 2000) and 24.9°C (October 1998). The total monthly rainfall varied from 230 mm (April 1999) to 1723 mm (December 2000).

Homogeneity of test plots. To examine whether the test plots, where propagules were laid out, were homogeneous with regard to abiotic factors, both light conditions and soil acidity were recorded. Measurements of light conditions were taken for each experimental plot. With a Gossen Luxmeter the amount of light falling on the ground was measured for *Microcos* 20 times, *Neoscortechinia* 14 times, *Syzygium* 10 times and *Platea* 7 times, with readings spread over the whole day. The number of counts was proportional to the period of observation. Soil acidity was checked with a Hellige Pehameter twice in each plot. Conditions in both *Ficus* and *Pygeum* plots went unrecorded.

One could assume that a higher illumination leads to better growth and survival. Therefore plots with different survival rates were checked for different amounts of light reaching the ground. Plots did not differ significantly from each other. Similarly, all plots showed about the same acidity (between pH 4 and 4.5). Accordingly, we assume that soil condition was similar at all plots in the study area, which is not surprising in view of the homogeneity of its level ground everywhere.

Selection of species, trees, fruits and seeds. Six fruiting individuals of six different species were selected for study. The six trees were 12–30 m high and were canopy or subcanopy trees. Nearest neighbor adult conspecifics were at least 100 m away. Each species was represented by several individuals in the area. All trees bore ripe fleshy fruits. It was assumed that their fruits were eaten and dispersed by birds and bats because of their fleshy pulp, which was confirmed by locals who had observed birds and bats eating fruits of five (all but *Ficus*) and three (*Syzygium, Ficus, Pygeum*) species, respectively. Our own observations indicated that only three and two of the six species selected were indeed eaten respectively by birds and bats. Thus we assumed that fruits had been temporarily rejected due to their abundance during the study period, or there had been a drastic decline in bird density. For each species 30 randomly chosen fruits or seeds were measured (length and weight) and assessed for ripeness (data not shown). Damaged or infested fruits and seeds were discarded. Fruits or seeds were picked or collected with fruit traps. Cotton sheets (1.1 m x 1.1 m) were suspended from surrounding vegetation 1 m above ground. The traps were emptied every morning and evening at 06:00 h and 18:00 h for up to three days.

Species and propagule placement. A propagule is here any individual fruit regardless of its stage of development, thus including whole fruits, seeds, and seedlings. To prevent any contamination with insect repellent from our skin we avoided touching fruits or seeds with bare hands. The number of seeds placed per quadrate plot varied between tree species because of differences in crop size and accessibility of fruits. Plots were checked at least weekly for varying time periods (see Results). We recorded the number of fruits/seeds, the general condition, germination stage,

length of seedling, number of leaves, longest leaf length, length of radicle, and signs of damage. A seed was scored 'survived' when it was undamaged or had developed into a seedling appearing viable. A fruit was judged 'survived' when it had not been eaten or covered by fungus.

Microcos stylocarpa Burret, Tiliaceae: The fruits of *Microcos* are yellow-orange, their pulp is juicy and fibrous and adheres strongly to the seed. Therefore only fruits were used for the experiment. On the experimental tree, 224 fruits, and an additional 128 fruits from a different *Microcos* tree, 200 m distant, were collected and used for the experiment. The use of further fruits from a different individual was necessary due to difficulties collecting sufficient numbers.

Arrangement of plots was along a system of three radii, radiating in different directions from the parent tree. Directions were dictated by the topography of the terrain, in avoiding slopes along which rains would have misplaced the seeds in the plots.

Along each radius three experimental square plots of size 50 x 50 cm were set up at the distances 'under parent', '30 m', and '50 m' away from the trunk (see Fig. 1). Fruits from the second tree were deposited solely along one radius of their own. Due to a strong bend of the trunk the crown did not project down to the ground around the trunk, therefore two additional plots were set up beneath the trunk. We wanted to check if fruits close to the tree trunk experience a different fate from those lying under the crown. Each experimental plot was provided with 32 fruits. The position of a plot, marked by a peg, contained 32 fruits. Along one radius of their own, fruits of the second *Microcos* tree were placed.

Neoscortechinia philippinensis (Merr.) Welzen, Euphorbiaceae: The fruits of *Neoscortechinia* are green, consisting of one brown seed covered by a bright red aril. The exocarp opens in four valves and reveals the aril. The seed hangs on the valves connected through a funiculus at least as long as the seed. Sixty seeds covered with an aril were collected and used for the experiment. Fruits were eaten by at least four different bird species (*Hypsipetes philippinus*, *Penelopides panini*, *Phapitreron leucotis*, and *Macropygia phasianella*). Birds were observed defecating or regurgitating the seeds (C. Fink-Schabacker pers. obs.). The tree regularly occurs in low elevation forest (Merrill 1967).

Fruits were deposited along two radii with three experimental plots each of size 30 x 30 cm at the distances 'under parent', '30 m', and '50 m' away from the trunk (see Fig. 1). Each experimental plot, marked by a peg, contained 10 fruits.

Syzygium sp., Myrtaceae: The blackish-blue fruit of *Syzygium* contains a single seed that is encased by a basket-like structure often found on the forest floor. We used two radii starting at the parent tree. Experimental plots of size 30 x 30 cm were set up pairwise, i. e., on each side along each radius at the distances 'under parent', '40 m', '70 m', and '100 m' (see Fig. 1). The plots on one side of each radius contained fruits, the plots opposite to these seeds. Each plot contained 15 fruits or seeds so that in total 120 seeds and 120 fruits were laid out.

Fruits stuck out from the crown, usually a characteristic of bat-dispersed fruits (van der Pijl 1972). During 31 hours of daylight observation and 6 hours of night observation no bird or bat was observed picking fruits, even though fruit bats came very close to the fruits and were caught a short distance from the tree.

Platea excelsa var. *borneensis* (Heine) Sleum., Icacinaceae: The fruits of *Platea* are blackish when ripe and red when unripe. The drupe consists of a seed, covered by a hard walnut-like endocarp. The seed turns blue when it comes in contact with air. The tree is regularly found in dipterocarp forest up to 2000 m a.s.l. (Sleumer 1976).

Fruits have been eaten by *Penelopides panini*. We observed a rat (*Rattus* sp.) (pers. obs.) eating the contents of the fruit. Two hundred fruits were collected and the stones (referred to here as seed) placed in 40 experimental plots of size 50 x 50 cm. We used four radii, radiating in different directions from the parent tree. On each side along each radius at the distances 'under parent', '30 m', '50 m', '70 m', and '100 m' (see Fig. 1) an experimental plot was set up and provided with five seeds.

Ficus sp., Moraceae: Ripe syconia (the 'fruits' of a fig) of this species are green and contain hundreds of tiny seeds. We did not see other visitors except fruit bats (J. Reiter pers. obs.). With their typical feeding behavior of both ejecting and defecating seeds, bats 'free' seeds from being permanently enclosed in fruit pulp. To account for this, we planted seeds defleshed manually by the experimenter (as was the case in *Pygeum* (see below)).

Along radii, following largely the four points of the compass, plots were set up at the distances 'under
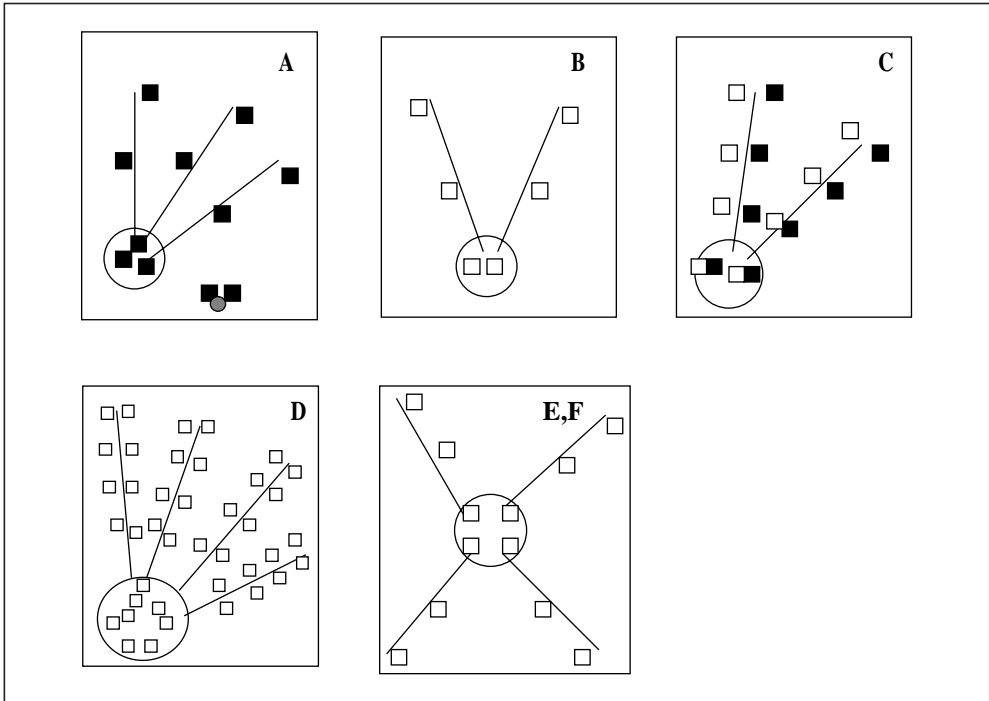
FIG. 1. Details of the experimental design for the distance experiment. **A** *Microcos stylocarpa*, **B** *Neoscortechinia philippinensis*, **C** *Syzygium* sp., **D** *Platea excelsa*, **E** *Ficus* sp., **F** *Pygeum vulgare*. Black squares indicate plots with fruits, empty squares show plots with seeds or seeds covered with a thin aril (**B**). Circles symbolize the tree crown, gray circle the trunk. In **A** two extra squares have been set up beside the trunk base.

parent', '40 m', and '80 m' away from the trunk (Fig. 1). Each plot of size 50 x 50 cm contained 50 seeds.

Pygeum vulgare (Koehne) Merr., Rosaceae: These fruits turn from pale green to red, and finally to black when fully ripe. A single, non-adhesive seed is found in each drupe. The pulp is soft but not very juicy. At least one bird species, *Penelopides panini*, and one bat species, *Ptenochirus jagori*, were observed feeding on the fruits (J. Reiter pers. obs.).

Again, four radii and experimental plots of size 50 x 50 cm were used. Plots with 22 manually defleshed seeds were each placed 'under parent' as well as at '30 m' and '60 m' from the mother tree.

Period of observation. Monitoring of *Microcos* lasted 26 weeks, of *Neoscortechinia* 20 weeks, of *Syzygium* 18 weeks, of *Platea* 14 weeks, of *Ficus* nearly 14 weeks, and of *Pygeum* 15 weeks.

Miscounts. If, during monitoring of plots, a seed or seedling was overlooked but appeared in a later count, it was assumed that it had been temporarily covered with litter, soil or mud. Excluding plots beneath the parent crown, propagules thus missing were later included in the calculation of the earlier count. We regard this procedure as acceptable because the probability of a seed falling onto a plot after the peak of fruiting appeared minuscule.

Statistical analyses. Differences in survival curves among the different distance classes of each tree were statistically examined in a pairwise design with a Mantel test. An analysis using contingency tables was inappropriate as it would have required independence of data. To the extent that progeny of the same tree may yield survival data that are interdependent, chi-square statistics would not be valid. To account for the va-

riation in the number of replicates (radii) among tree species, P's have been corrected using the sequential Bonferroni test (Rice 1989, based on Holm 1979).

RESULTS

Germination. Seeds of different species germinated at different times after being deposited alongside the radius. The walnut-like seeds of *Platea* started to germinate after 5 weeks, as did the seeds of *Microcos*. Fruits of *Syzygium* germinated after 3 weeks, whereas it took only one week for the naked seeds to germinate. The seeds of *Neoscortechinia* showed first signs of germination after 3 days. All *Ficus* seeds had germinated by the end of the second week, while this had occurred with 70% of the *Pygeum* seeds by the end of the third week.

Mortality. The causes of mortality varied among species. Most seeds of *Microcos* and *Platea* suffered from insect frass hollowing the seeds, whereas seedlings of *Neoscortechinia* mostly fell victim to pathogens, clearly visible by necrotic patches on the stems. Over half of the fruits and seeds of *Syzygium* disappeared after the third week. Those seeds of *Platea* lying directly under the crown were mostly destroyed by rats. *Ficus* seeds suffered an extremely high mortality by being eaten or carried away by ants. Seeds of *Pygeum* succumbed in the seedling stage largely to insects, less to pathogens and small mammals.

Overall survival. In general all species showed a high initial mortality rate in the first two weeks. Within 14 weeks only 9.2% of *Microcos* propagules survived. *Neoscortechinia* seeds had a slightly higher mortality, with a survival rate of 6.7%, as did the seeds and fruits of *Syzygium*; only 5.2% of *Ficus* seeds survived to week 3, a similar proportion (4.2%) of *Syzygium* to week 14. *Platea* had the highest survival rate of all six species with 24.5% of the propagules surviving week 14, while *Pygeum* ranked intermediate in a similar time period. These species differences will yield insights regarding the 'escape hypothesis' when being broken down into distance-from-parent classes (next section).

Survival and dispersal distance
Microcos: After 26 weeks of monitoring only 5 of 11 plots showed surviving seedlings. Out of a total of 388 fruits laid out, 24 seedlings survived, as well as an additional 36 fruits that had fallen accidentally into
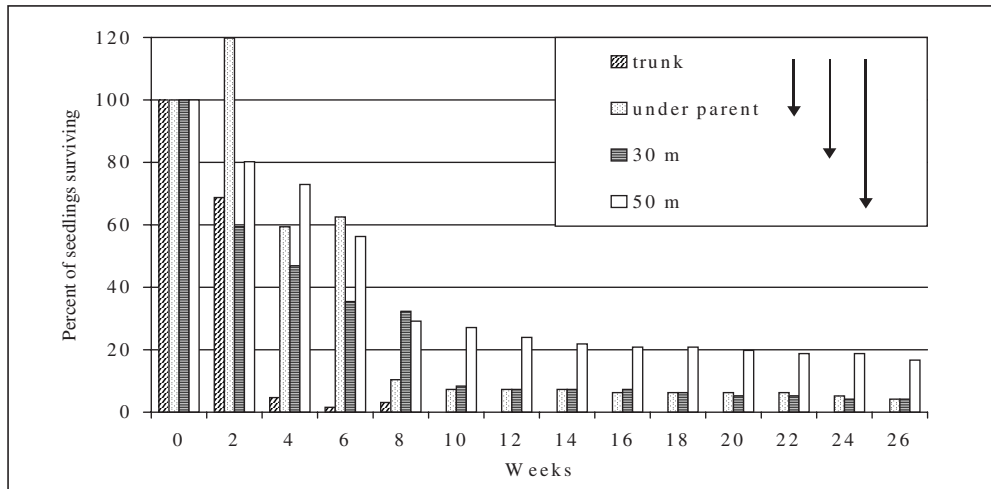

FIG. 2. Percent of surviving seedlings of *Microcos stylocarpa* at distances 'under the parent tree', 30 m, and 50 m away. Two additional plots were set up near the trunk base. An increase in number of seeds under the parent tree in week 2 was caused by natural fruit fall. Black arrows indicate significant differences in survival between distances ($10^{-5} < P \leq 0.001$).
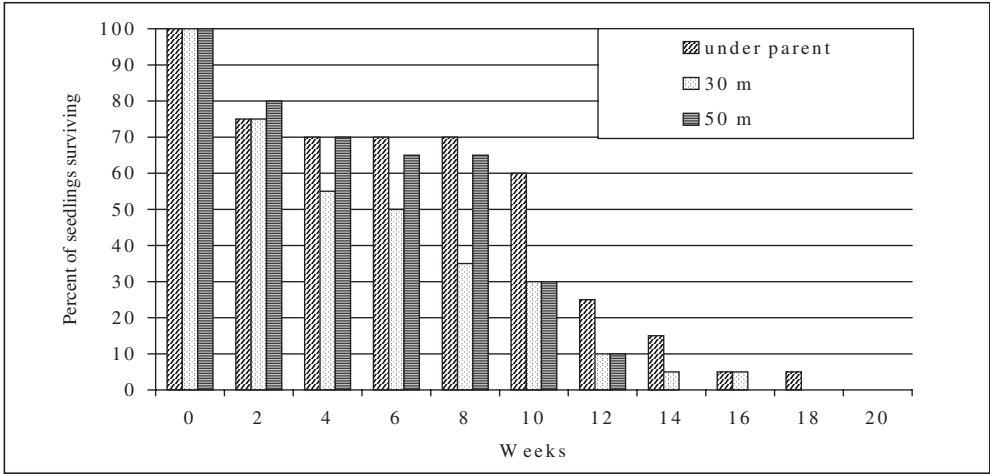
FIG. 3. Percent of surviving seedlings of *Neoscortechinia philippinensis* at distances 'under the parent tree', 30 m, and 50 m away.

the plots beneath the crown (see Fig. 2). The fruits laid out beside the trunk died or disappeared within 8 weeks; there was a loss (95.3%) of all but three propagules after week 2. The largest number of seeds survived at the 50 m distance. But the seedlings were not those of the focus tree but the propagules of the second *Microcos* tree farther away. Of the 96 seeds in the 50 m plots, 14 seeds of the latter survived week 26. In contrast to the high survival rates of seedlings at this distance from this second tree, the offspring of the focus tree showed lower survival rates. Only 2 seedlings survived week 26. Both under the parent and 30 m away 4 seedlings each survived. Comparing the seedling survival curves (Mantel test), we found significant differences between the distances trunk–under crown ($P \le 10^{-5}$), trunk–50 m ($P \le 10^{-5}$), and trunk–30 m ($P \le 0.001$). Other pairwise comparisons were not statistically significant.

Neoscortechinia: No seedling survived week 20. Ants removed all arils within the first day. Seeds germinated quickly and seedlings grew up to 10 cm within four weeks. Seedlings growing under the parent survived longer than those at other distances (see Fig. 3) and the number of seedlings surviving under the parent was higher than the survival rates 30 m and 50 m away, though the differences are statistically non-

significant. The initial losses could be attributed to insect infestation, whereas unidentified pathogens accounted for losses later on. It was also observed that primary leaves suffered heavier losses from herbivory than secondary leaves.

Syzygium: Over half of the fruits and seeds (57.1%) of the *Syzygium* tree disappeared within the first two weeks. After four weeks survival rates decreased to an overall proportion of 10.4%, which comprized 9 fruits and 11 seeds (see Figs. 4, 5). There was no significant difference in the proportion of seedlings surviving when comparing cohorts 'under parent' to 'far away from parent' ($\chi^2 = 0.172$, d.f. = 1, $P > 0.4$). After 18 weeks of monitoring, 7 seedlings in seed plots and only one seedling in a fruit plot had survived. Seeds had a significantly higher survival rate than fruits ($\chi^2 = 0.025$, d.f. = 1, $P < 0.025$). Statistical analysis of mortality curves (Mantel test) showed significant differences between the distances 'under parent' –40 m ($P \le 10^{-5}$) as predicted, but the trend was reversed when looking at 'under parent'–70 m ($P \le 10^{-5}$) and 'under parent'–100 m ($P \le 0.002$) for fruit plots (Fig. 4). Tests of the seed plots showed significant differences between 40 m–100 m ($P \le 5 \times 10^{-4}$) and 70 m–100 m distances ($P \le 0.008$), again as predicted (Fig. 5).
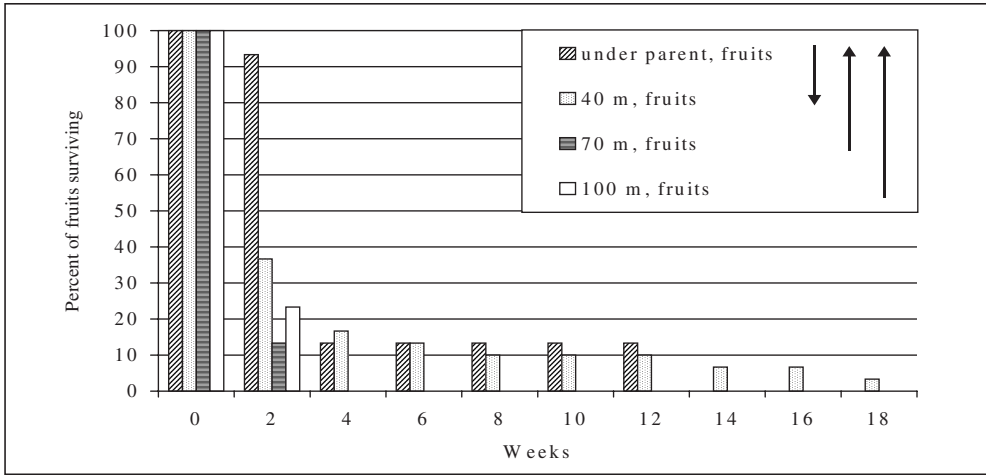
FIG. 4. Percent of seedlings of *Syzygium* sp. surviving at distances 'under the parent tree', 40 m, 70 m, and 100 m away. Seedlings developed from plots with fruits. Black arrows indicate significant differences in survival between distances ($10^{-5} < P \leq 0.002$).

Platea: Seeds were attacked by insects or, especially under the parent, destroyed by seed-eating mammals. The effects of insects could easily be detected by holes in the testa.

Due to the hard testa it took up to five weeks until first signs of germination were detected. Only 8 of 49 seeds surviving week 14 germinated. No seed survived under the parent (see Fig. 6). The proportion of seeds
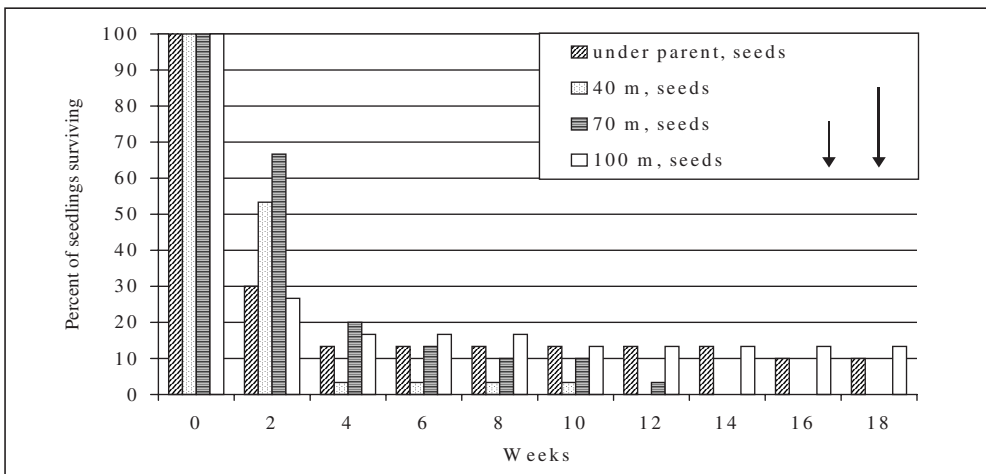

FIG. 5. Percent of seedlings of *Syzygium* sp. surviving at distances 'under the parent tree', 40 m, 70 m, and 100 m away. Seedlings developed from plots with seeds. Black arrows indicate significant differences in survival between distances ($5 \times 10^{-4} < P \leq 0.008$).
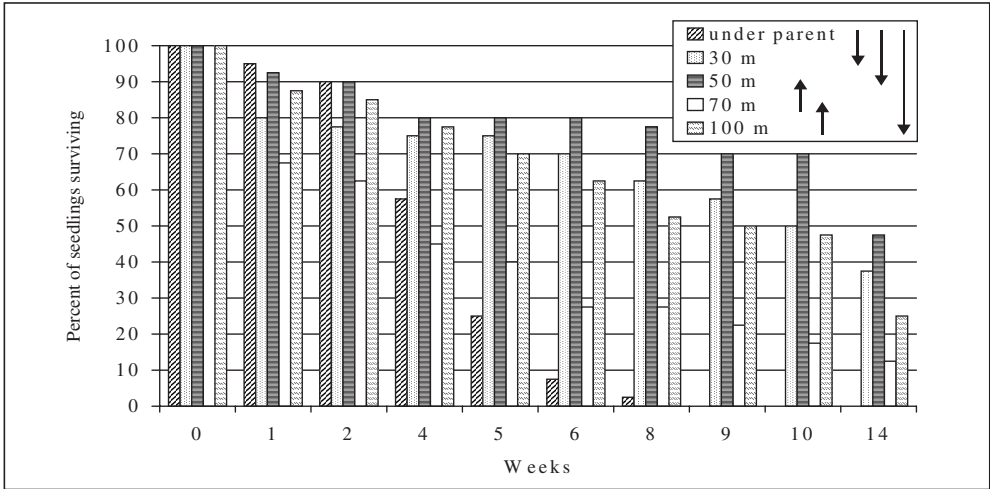
FIG. 6. Percent of surviving seedlings of *Platea excelsa* at distances 'under the parent tree', 30 m, 50 m, 70 m, and 100 m away. Black arrows indicate significant differences in survival between distances ($10^{-5} < P \leq 0.003$).

surviving far away from the parent was significantly higher than the proportion surviving under the parent ($\chi^2 = 14.92$, d.f. = 1, $P < 10^{-5}$). Significant differences between the mortality trajectories were found in the following distances, when using the Mantel test: 'under parent'–30 m ($P \leq 0.002$), 'under parent'–50 m ($P \leq 10^{-4}$), and 'under parent'–100 m ($P \leq 3 \times 10^{-4}$), as predicted by the escape hypothesis. By contrast, this trend was reversed at the greater distances: 50 m–70 m ($P \leq 0.001$) and 70 m–100 m ($P \leq 0.003$).
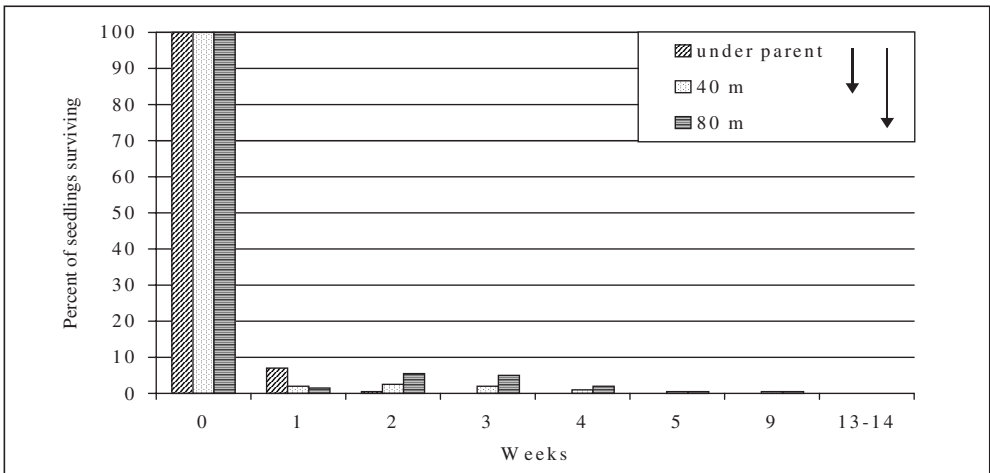

FIG. 7. Percent of surviving seedlings of *Ficus* sp. at distances 'under the parent tree', 40 m, and 80 m away. Black arrows indicate significant differences in survival between distances ($10^{-5} < P \leq 3 \times 10^{-4}$).
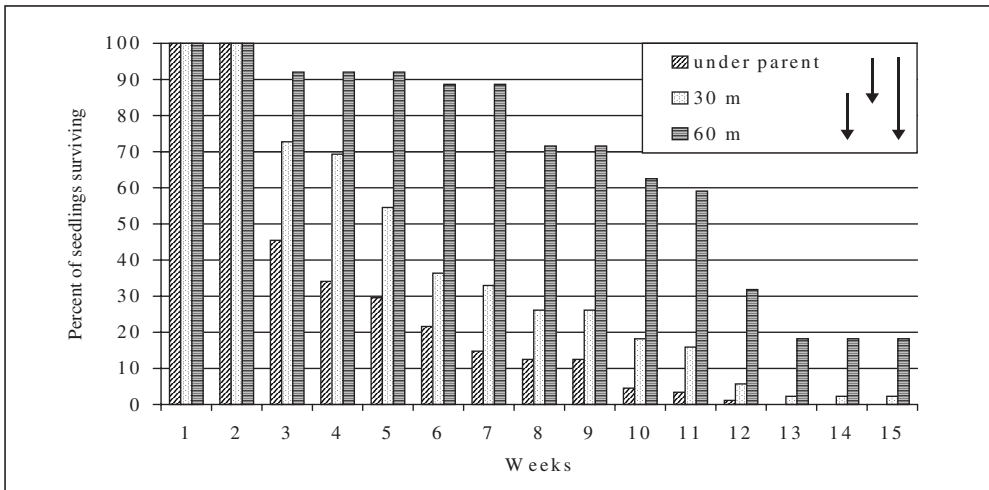
FIG. 8. Percent of surviving seedlings of *Pygeum vulgare* at distances 'under the parent tree', 30 m, and 60 m away. Black arrows indicate significant differences in survival between distances ($10^{-5} < P \leq 10^{-4}$).

Ficus: Germinated *Ficus* seeds were only recorded within the first two weeks (Fig. 7). Ants were seen carrying seeds away. Additionally, seeds with holes indicated that ants heavily fed on intact ones. Both observations indicate that most of the sown seeds are likely to have fallen victim to this seed predator (and disperser?) soon after the trial had started. Seed mortality reached 94.8 % after two weeks. After week 3, only plots at the distances '40 m' and '80 m' still contained seedlings. In comparing seedling survival curves (Mantel test), significant differences were found as predicted, with seeds 40 m and 80 m away from the trunk having higher survival rates compared with those under the parent ($P \leq 10^{-4}$ and $P \leq 3 \times 10^{-4}$ respectively). Moreover, seeds at 80 m had higher levels of germination than seeds half the distance away from the parent, possibly due to chance ($P > 0.7$).

Pygeum: Of 264 sown seeds, 70 % germinated between the second and third week (Fig. 8). Seedling mortality varied among distance classes. After 12 weeks, the only remaining seedling under the parent tree died. After 15 weeks, two seedlings (2.3 %) could still be recorded 30 m away from the trunk, this also being true for 16 seedlings (18.2 %) at a distance of 60 m. By this time, seedlings grew up to > 20 cm. Seedling mortality under the mother tree was highest between

week 2 and 3. All pairwise comparisons of mortality curves revealed significant differences among the distances 'under parent'-30 m, 'under parent'-60 m, and 30 m-60 m ($P \leq 10^{-4}$ in all cases), as predicted by the 'escape hypothesis'.

DISCUSSION

Density-independent support of the Janzen-Connell model. In this study Janzen´s (1970) hypothesis, which predicts that survival of propagules increases with increasing dispersal distance, was tested. However there seems to be no straightforward answer to this question. The results for four of the six tree species examined (*Microcos, Platea, Ficus, Pygeum*) clearly support the hypothesis. This trend is paralleled by the survival pattern in *Syzygium* seed plots beyond the crown area. This finding is extremely important since it must be due to a genuine distance-survival effect; densities were kept constant across all plots of an experiment. The accidental increase of the original cohort 'under parent' in *Microcos* by week 2 was probably of minor importance in terms of density. First, the increase amounted to only 10 % of the original cohort laid out. Second, it could have affected only one of three comparisons for this species, all in support of the distance-survival effect (Fig. 2).

It should be remembered that correlational studies had pinpointed propagule density, and by implication density-dependent mortality, as the crucial and necessary variable underlying the Janzen-Connell model (Clark & Clark 1984, refs. in Howe & Miriti 2000). Our finding is the first support for the escape hypothesis in the Old World tropics and parallels other, though less powerful tests in the New World by Schupp (1988) and Howe *et al.* (1985). Schupp demonstrated in *Faramea occidentalis* that dispersal distances as short as 5 m can significantly increase seed survival.

In *Neoscortechinia*, mortality far away from the parent was higher than under the parent tree. This would be a clear negation of the escape hypothesis had not all seedlings died or disappeared after week 20. The latter is a surprising result and should be re-examined with a larger number of *Neoscortechinia* trees and seeds.

The pattern of underlying mortality. Evidence is accumulating that propagule mortality is at least partially due to host species-specific pathogens, e.g., fungi (van der Putten 2000; see also Augspurger 1984, Augspurger & Kelly 1984). Pathogen-caused mortality would be consonant with our finding that survival per plot is not density-dependent. As opposed to mobile seed predators, pathogens are stationary and cannot be attracted over distances to a patch rich in seed, such as the one under the crown (e.g., Wilson & Janzen 1972). A pathogen-driven mortality would predict that survival would increase uniformly with distance, as actually observed most clearly in, e.g., *Pygeum*. The activity of mobile predators would suggest a threshold, with survival suddenly increasing beyond the crown area because of the attraction of a large crop under the crown that we did not control for. However, the survival pattern observed did not reveal such a threshold effect, which, in spite of searching, also remained elusive in earlier studies (Clark & Clark 1984). Similarly, anomalies in the survival distance pattern are also best explained by small-scale variation in attack from pathogens; the seedlings of *Platea* showed the highest survival rate at the 50 m distance, with survival again decreasing significantly at the 70 m or 100 m distance. Collectively, the evidence available lends support to a density-independent spatial mortality pattern.

Aside from seed predation, intraspecific competition has been invoked as an underlying cause of the survival distance effect under discussion. This idea would receive support if mortality were positively density-dependent. The idea can be rejected in the present case since the same evidence supporting density-independence would also argue against intraspecific competition as the underlying cause of the Janzen-Connell model.

Because of fruit scarcity, additional fruits of a conspecific *Microcos* tree were used in the experiment. They showed a singularly better survival at the 50 m distance, which was not evident at the same distance on plots of the focal parent tree. We find it hard to explain why there should be a better survival rate for conspecific, non-sib offspring 50 m away from the focal tree, especially since the sib and non-sib cohorts did not differ at any of the other distances. In addition, the escape hypothesis is further supported by the focal tree's cohort at 30 m surviving better than under the crown and the trunk.

Based on their results for *Platypodium elegans*, Augspurger and Kelly (1984) gave a possible explanation for better survival rates of non-sib offspring. They speculate that there is a host-pathogen coevolution that leads to parent-specific and hence site-specific pathogens. Thus a parent's offspring should be more vulnerable and show higher mortality near the parent tree. This would explain the result of non-sib offspring being less vulnerable and having higher survival rates 50 m away, but the idea is not supported by high mortalities, similar to those of the parent's offspring under the crown, near the trunk, and 30 m away. The fact that there is a higher chance of survival with increasing distance is rather supported by the distance effect, which should also benefit the parent's offspring but did not show up in this experiment.

The fruits of *Microcos* laid out close to the trunk all disappeared or died within 8 weeks. Statistical analysis shows that there are significant differences in survival rates between trunk–parent, trunk–50 m, and trunk–30 m. This clearly supports the distance effect. The fact that survival curves under the crown, compared with plots 30 m and 50 m away, did not yield similar differences is an effect best ascribed to chance. One would also expect a strong survival difference between 'under the crown', where most fruits are, and increasing distance. Taken together, the data nevertheless strongly indicate the proposed distance effect. The death of about 95 % of seeds around the trunk during the first three weeks might be an effect of allelopathics secreted by the roots or of soil impoverished by the parent roots.

It became clear that propagule mortality is especially high in the first weeks after dispersal, as previously shown by Kachi *et al.* (1993). Howe *et al.* (1985) found mortality rates of 99.2 % in *Virola surinamensis* seeds in the first 12 weeks after being deposited. Therefore numbers of seeds used in experiments of this kind have to be very high.

For *Syzygium* it was shown that fruits have smaller survival chances than seeds. Rotting fruits emanate a strong smell and hence can be more easily detected by animals. Also strikingly colored fruits can more easily fall victim to animals hunting by sight. This result hints at the possibility that survival rates could have been higher for *Microcos* propagules than actually observed, since data were derived from seedlings grown from fruits. If this were the case, the escape hypothesis would have been strengthened even more than suggested above; the homogenizing effect of fruit predation may have blurred between-cohort variation (see Terborgh *et al.* 1993).

For wind-dispersed trees, Augspurger (1984) and Augspurger and Kelly (1984) found better survival chances in light gaps. This may be especially true for lightweight seeds showing more resemblance to seeds of secondary forest. In this study the possible influence of different light conditions or soil acidity could be ruled out. No experimental plot got significantly more light than others nor did soil acidity vary across plots.

Community effects. Our confirmation of the Janzen-Connell model is of great importance for the understanding of forest tree communities. Hubbell (1980) suggested that the seed fall under the parent tree is so overwhelmingly large as to negate any community effect of seed dispersal. Accordingly, recruitment of progeny under the parent would be strong enough to prevent other, rare species from settling there. This idea is falsified by our finding that mortality under the parent is so high that in five of the six species tested no survivors remained. Even in the deviant situation of part of the *Syzygium* experiment (Fig. 5) the number of survivors under the crown decreased so drastically that their survival as a cohort must be in question. In other words, the per capita mortality of the undispersed cohort must be high enough to open up space for other community members, thereby falsifying Hubbell's (1980) assumption. If common, the high under-the-parent mortality of the parent's propagules should have a far-reaching community effect. It would increase species diversity by allowing rare species to settle in the 'death zones' of other species (see also van der Putten 2000).

Similarly, in spite of recent skepticism against such community-wide effects explicable by the Janzen-Connell model (Howe & Miriti 2000), the model can also explain the spatial distribution and density regulation of tree species in a tropical forest (Terborgh 1992 *fide* Hubbell).

General conclusion. This study demonstrates for four species that there is a higher chance of propagule survival if the seed is dispersed and escapes the parent's vicinity, thereby supporting the Janzen-Connell model. For two other species results are not very clear-cut and warrant re-examination. Yet other determinants of seed establishment, e.g., colonization of a suitable site (Howe & Smallwood 1982, Willson 1993) and leaf litter composition may affect survival as well (refs. in Clark & Clark 1984, Molofsky & Augspurger 1992). Furthermore, results are best explained by spatially patterned mortality factors operating in a density-independent manner, thus ruling out a major tenet of the Janzen-Connell model.

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