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Spatial and temporal patterns of seed attack and germination in a large-seeded neotropical tree species

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Abstract It has long been argued that seed dispersal enhances recruitment in tropical trees by allowing offspring to ‘escape’ strong density/distance-dependent attack by insects, pathogens and rodents. Here we examined the effects of canopy openness and parent-offspring distance upon the frequency and timing of *Chlorocardium rodiei* seed attack and germination within a 15-ha plot of Guyanan tropical rain forest. Seeds were artificially dispersed beneath parent trees, in the understorey away from trees and in gaps. Analysing our data from an 85-week period of regular monitoring, we found that the main spatial gradients, canopy openness and distance to nearest adult conspecific, do not lead to differences in the final number of seeds attacked by infesting scolytid beetles or rodents. The timing of beetle attack, however, varied along the distance gradient and this difference affords seeds at further distances a ‘window’ in which to germinate and produce a seedling before attack. Canopy openness was not a good predictor of rooting success, but distance was strongly associated with root and shoot formation success and the mean time to shoot formation. There was a strong negative effect of distance on the likelihood of a seed being colonised by scolytid beetles prior to removal by rodents and shoot failure was

strongly associated with prior infestation. We believe these results bring a key point to bear on the well-established notion of distance-dependent attack on seeds in tropical rainforests, viz. that seed characteristics (size, germination syndrome) and the timing of attack may be more important in explaining patterns of early seedling recruitment than distance. Our studies suggest that advantages accrued through dispersal in species like *Chlorocardium* will depend heavily on the ‘race’ between seed germination and attack. In the case of *Chlorocardium*, the ‘race’ can be lost at considerable distances due to its prolonged dormancy and the temporal fluctuations in fruitfall and rainfall which influence attack and germination. The results presented here suggest that the lag between seed attack and germination in tropical trees can regulate the influence of parent-offspring distance on cohort recruitment at this life history stage.

Key words *Chlorocardium* · Dispersal · Rodent · Scolytid beetle · Treefall gap

Introduction

Unlike germinated siblings, seeds cannot redistribute their biomass in space (e.g. specific leaf area, root zone), attempt to compensate for lost biomass through regrowth nor alter the temporal distribution of their tissues (e.g. flushing) or the chemical composition of these tissues in response to changes in their surroundings. The ‘fixed’ nature of response increases the likelihood of mortality once attacked and heavy losses at this early stage can substantially influence the population dynamics of species (Rees 1997).

Seed mortality is predominantly due to attack by vertebrates, invertebrates and/or pathogens or unfavourable abiotic conditions which hinder germination. The distance from conspecific adults (Janzen 1970) and level of canopy cover (or gap size) (Schupp et al. 1989) have been suggested as explanations for the spatial variation in germination and seed predation in tropical for-

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ests. At the same time, seasonality of fruitfall and rainfall have been linked to the temporal variation in predation (e.g. Schupp 1990) and germination (e.g. Garwood 1983).

Spatial and temporal variation in exogenous factors influencing attack and germination interplay with the phenotypic traits of seeds to produce a mortality pattern. Attack does not necessarily equate with predation in this case because respective traits of the putative predator, such as foraging behaviour and body size, and prey, such as dormancy and seed size, can alter the likelihood that attack is lethal. Attack can also result in dispersal (e.g. unrecovered caches) or simply reduce seedling size in proportion to the amount of seed mass lost (Hammond and Brown 1998), depending on the species attributes. If these attributes reduce the probability of predation or germination failure, then fewer offspring will succumb to early mortality. Low seed survival and poor germination should occur more frequently when seed size, dormancy and dispersal syndromes are 'discordant' with current mortality processes (sensu Levin 1992). In fact, these attributes are often interrelated (Leishman and Westoby 1994) and together they interact with changes in spatial and temporal effects of mortality factors to define a recruitment trajectory for the cohort. For example, the limitations imposed on dispersal distance by seed size are thought to be important, because movement away from adult conspecifics can often reduce the likelihood of density/distance-dependent predation by insects (Janzen 1970) and pathogenic fungi (Augspurger 1983).

A number of field experiments have been performed to determine the impact of attack and dispersal distance on large-seeded, neotropical species (e.g. Howe et al. 1985; Forget 1990) and the influence of distance and light environment on seed survival of smaller-seeded species (e.g. Augspurger and Kelly 1984; Schupp 1988) around individual adult trees. Overall attack on seeds has been assessed as a function of adult density at larger spatial scales but without describing the temporal process through which this final outcome was achieved (Schupp 1992). Rarely has the relationship between the spatial and temporal patterns of attack and germination for large-seeded canopy tree species been assessed concomitantly at habitat-level scales, though variation in germination and attack at this scale is more consistent with population-level effects. Moreover, the germination timing and seed size of a species are rarely implicated in patterns of attack and germination.

In this paper, we examine the role of dispersal distance and canopy openness on the seed survival and germination of a large-seeded, neotropical canopy tree, *Chlorocardium rodiei* (Schomb.) Rowler, Richter and van der Werff (syn. *Ocotea rodiaei*) (Lauraceae) (henceforth *Chlorocardium*). We tested several hypotheses concerning *Chlorocardium* seed ecology by following the fate of a single, artificially dispersed cohort from the moment of implantation until all surviving individuals had successfully reached the seedling stage. In so doing, we were able to evaluate the relative significance

of spatial and temporal gradients on patterns of seed attack and germination. We approached the problem by asking: what are the effects of variation in canopy openness and distance from nearest adult conspecific on (1) *Chlorocardium* seed attack by rodents and/or insects? (2) the incidence of attack from moment of dispersal until all surviving individuals had reached the seedling stage? (3) final germination success? (4) germination time? and, finally (5) the relationship between the spatial and temporal patterns in attack and germination? We also assessed whether germination and attack were responsive to smaller-scale spatial variation within gaps.

Methods

Study site and species

The study was conducted at Mabura Hill, Guyana (5°13'N, 58°48'W, 100 m above sea level). The region receives an annual rainfall of 2400–3000 mm and has a mean annual temperature of 25°C. Most rainfall occurs from May to August and November to December, though monthly rainfall rarely drops to less than 60 mm. The topography is highly dissected, composed of the southernmost projections of Pleistocene sand deposits overlying a highly weathered Precambrian crystalline base complex and less weathered Mesozoic dolerite dykes and sills. Further details of the climate, soils and geology of the study area can be found in Ter Steege et al. (1996).

All *Chlorocardium* trees >10 cm dbh were identified in a 15-ha plot and their positions located on a 25 × 25 m grid. Mean (±SE) density of *Chlorocardium* (>10 cm dbh) within the plot was 12.2 ± 2.5 trees/ha. However, the population showed strong clumping at this scale (variance: mean of nearest neighbour distances = 2.34) with the mean (±1 SD) distance between nearest neighbours being = 3 × the crown radius (18.7 ± 12.9 m) (Fig. 1A). In August–September 1991 all gaps (sensu Brokaw 1982) were measured and their positions located within the plot. Mean (±SE) gap size was 95 ± 16 m² ($n = 48$), the largest being 558 m² (Fig. 1C).

Chlorocardium is a monoecious canopy tree endemic to the eastern part of the Guiana Shield. It is a common codominant in many well-drained areas covered by brown sand (FAO: haplic Ferralsols) and lateritic (dystric Leptosols) soils, where it can reach densities of 84 and 40 stems (>10 cm dbh) ha⁻¹, respectively (Fanshawe 1947; D.S. Hammond, unpublished data). This species has the sixth-heaviest seed (mean ± 1 SD = 65.5 ± 22.3 g fresh weight; Ter Steege 1990) of more than 280 woody species for which fresh seed weight has been measured in the study area (Hammond and Brown 1995; D.S. Hammond, unpublished data) and is thus one of the heaviest-seeded species in the Guianas. The single seed is enclosed in an indehiscent woody exocarp. Fruitfall generally peaks in February–March (Ter Steege and Persaud 1991), but interannual variation in the time of median fruitfall within some subpopulations can be high, ranging from January to April (Zagt 1997). The quantity of seed falling within a subpopulation can also vary three- to fourfold from year to year as some individuals fail to fruit (Zagt 1997; D.S. Hammond, unpublished data).

Seeds of *Chlorocardium* are attacked by a broad spectrum of rodent and insect predators, despite high concentrations of volatile secondary compounds common in the Lauraceae (see Janzen 1974). The microlepidopteran, *Stenoma catenifer* (Stenomatidae), commonly infests, prior to dispersal, (about 10% of seeds in a crop), while a beetle species in the genus *Sternobothrus* (Scolytidae) (henceforth *Sternobothrus*) attacks seeds after dehiscence and later bores into the stems of young seedlings. The seed embryo is often damaged by juvenile feeding, while parental galleries appear to house fungal growth. Fungus-feeding ants, *Trachymyrmex* sp. and

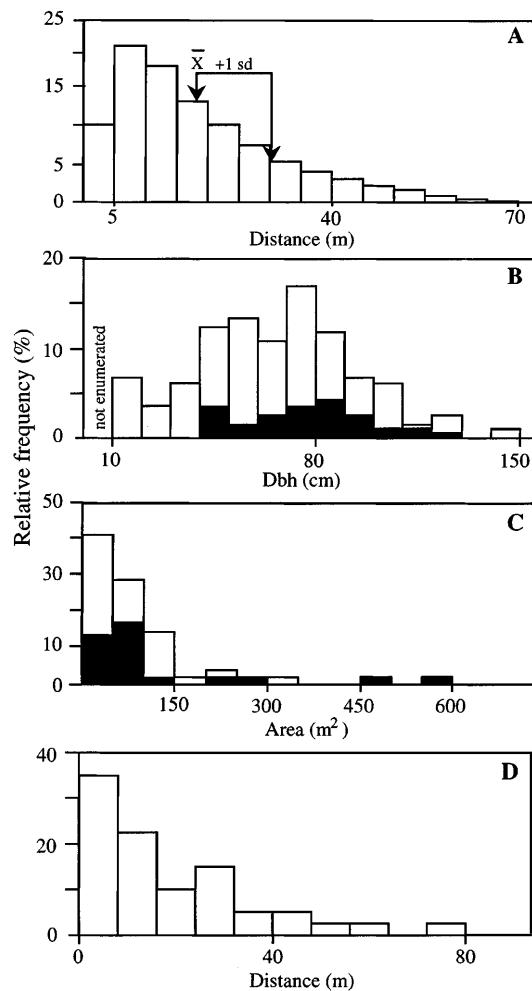


Fig. 1 Frequency distribution of *Chlorocardium* nearest neighbour distances (A), dbh size classes (B), gap sizes (C), and distances between implantation sites and nearest *Chlorocardium* adult within plot (D) as measured at the commencement of the study in March 1992. Filled bars in B and C represent the sites (gaps and individual adult trees) used in this study

Sericomyrmex sp. (Attini, Myrmicinae), will attack seeds and remove, often in their entirety, the bulky cotyledons. Based on the number of sightings, *Trachymyrmex* appeared to be the more common forager on *Chlorocardium* seeds (87% of sightings, $n = 46$).

The width of measured teeth marks on attacked *Chlorocardium* seeds are consistent with the measured incisor width of the (adult) caviomorph rodents, *Dasyprocta agouti*, *Myoprocta acouchi* (Dasyproctidae), *Agouti paca* (Agoutidae) and *Proechimys cuvieri* and *P. guyanensis* (Echimyidae) (henceforth *Dasyprocta*, *Myoprocta*, *Agouti* and *Proechimys*, respectively), though other less common echimyids and murids with similarly sized teeth may also attack seeds and seedlings. In order to assess the relative levels of attack by each of these main *Chlorocardium* predator/dispersers, teethmarks on naturally dehisced seeds beneath trees during March–June 1992 were measured and compared to measurements of the upper incisors taken from skulls.

Selection of implantation sites

The field experiment was designed to assess the effects of distance and microsite on levels of seed attack and germination success. The frequency with which attack and germination occurred was eval-

uated by selecting implantation sites, viz. gap and understorey, which were representative of the spectrum of microsite conditions. Twenty gaps were randomly selected from the existing set of gaps measured in the plot (Fig. 1C). Ten understorey sites beneath *Chlorocardium* trees (40 cm dbh) were randomly chosen from the set of all trees in the plot (Fig. 1B), while another ten sites which were beneath a closed canopy but 30 m away from a *Chlorocardium* tree were randomly selected from those 25 × 25 m grid cells which did not have any *Chlorocardium* trees (see Fig. 1D).

The ground within a gap is rarely homogenous, being variously covered by the crowns, boles and dislodged roots of the contributing trees. These different areas, or zones (sensu Uhl et al. 1988), within a gap often lead to different patterns of seed and seedling mortality within the same gap (e.g. Schupp 1988). To account for this potential source of variation, a set of paired implantation sites were placed in each of the twenty selected gaps; one site in the middle of the largest crown in the gap ('crown zone') and one site along the lower third of the tree bole ('trunk zone'). Zones were selected in a pair-wise fashion in order to minimise the variance due to differences between gaps upon the differences due to crown and trunk zone effects.

Hemispherical photographs were taken with a Sigma 8-mm lens at 50 cm above the centre point of each site following implantation. Percent canopy openness was calculated using WINPHOT 4 (Ter Steege 1994). This estimated canopy openness at both understorey and gap sites at day 1 of the experiment. Canopy openness above experimental blocks in gaps and the total area of the enveloping gaps were significantly correlated however (Spearman's $r = 0.65$, $P < 0.05$, $n = 20$). Subsequent in-growth at the sites, at both sub-canopy and canopy levels, is here considered a function of initial canopy openness. Thus, initial measurements were taken as a method of differentiating between trajectories in continuously changing microsite conditions within gaps.

Within-site treatments

Fresh, undamaged and uninfested seeds (pooled $n = 1920$) collected February–March 1992 from beneath fruiting trees ($n = 72$) were bulked and then randomly distributed between and within blocks consisting of treatments designed to exclude/suppress selectively, alone and in combination, the effects of rodent and insect consumers. Eight seeds were placed in two parallel rows (25 cm apart) of four seeds (15 cm apart) within each treatment (randomly assigned within each block to points 1 m apart). A small identification mark was placed on the outside of each seed near the point of cupule attachment, using a permanent-black marker. Thus, for the entire experiment, there were 60 implantation sites (gap and understorey blocks), each consisting of four treatments [caged + insecticide (CI), caged (C), insecticide (I) and no treatment (control) (NT)] with eight seeds per treatment.

Seeds were protected from rodent attack by encasing the group in a 65 × 50 × 20 cm green, plastic-coated metal mesh (4 cm²) cage encased in a 1-m tall by 65-cm radius cylinder of the same material. The sides of cages were buried about 10 cm below the surface and anchored by a metal hock at each end. Hinged panels of the same material on the top of the cage allowed access to the seeds throughout the study without increasing the risk of attack. Less than 2% of the 960 seeds placed within these cages were attacked by rodents.

Insect infestation upon seeds was reduced by the application of Dimethoate-40 (40% C₅H₁₂NO₃PS₂), a contact and systemic organophosphorus insecticide. An aqueous (dH₂O) concentration of 0.05% was applied at a rate of 2–5 ml per seed in a uniform spray. All seeds were treated in this way at monthly intervals for the first 12 months of the experiment. A bioassay at an understorey location showed the concentration used here to be no less effective than higher concentrations and to have no effects on germination when compared to untreated seeds. The application of insecticide appeared to interfere with rodent consumption in treatment I, despite the fact that the acute oral LD₅₀ (rat) is moderate at 291–325 mg/kg. It was felt these data were unreliable and they are therefore not

included in the analyses. To assess the effect of rodents on seed survival, time of attack and germination, the no-treatment group was used instead. Though this group was open to attack by all animals, the timing of rodent attack upon seeds within this treatment was not significantly dependent upon the timing of insect attack (least-squares linear regression on combined clear zones of gaps and understorey sites, square-root transformed, $n = 40$, $r^2 = 0.002$, $F_{1,38} = 0.07$, $P = 0.80$).

Damage and attack were scored for each seed at each measuring period. Scolytid attack was recorded as occurring when more than one entrance hole which penetrated beyond the woody exocarp were present. One entrance hole is often associated with 'prospecting' and rarely led to the level of damage associated with beetle colonisation in dissected seeds. Removal of seed mass was scored as rodent and/or ant attack based on tell-tale signs associated with each group of seed-eaters. Rodent attack is consistent with the presence of teeth marks and the removal of the chartaceous seed coat wedged between the woody exocarp and cotyledons. Seeds with cotyledons partially attacked by ants show a scalloped surface at the point of removal, due to the orbicular jaw movement of many individual ants. When removing all cotyledonous mass, ants do not remove the exocarp or seed coat.

Data analysis

Least-squares multiple regression was used to model the effect of canopy cover and distance on response variables at 85 weeks. Seasonality of germination and attack were analysed by first calculating the mean time until germination (MTG) and mean time until attack (MTA) for each replicate by using the equation constructed by Sork (1985), being:

$$\text{MTG or MTA} = \frac{\sum_{i=1}^{17} \frac{1}{2}(t_i - t_{i-1})n_i}{\sum_{i=1}^{17} n_i}$$

where t is the number of days since initial placement of seeds, i is the number of observations and n is the number of seeds germinating within the interval t_i and t_{i-1} .

We felt it was instructive to examine graphically, the probability of germination and attack over the course of the 85 weeks relative to larger-scale seasonal rhythms: (1) total fruiting, (2) *Chlorocardium* fruiting and (3) rainfall, which were not measured directly here. To do this, the probability density function value, $f(t)$, was first calculated for the midpoint of each census interval (Lee 1992). Excluding individuals which did not contribute to the overall incidence of germination or attack by 85 weeks allowed us to compare the temporal pattern of incidence independent of differences in overall success between distance classes. The probability density value was based on the total number of incidences which took place over the course of the study within a pooled set of seeds from the sites after they were grouped according to one of three distance intervals: (1) < 7 m from nearest reproductive adult *Chlorocardium*, ($n = 14$ sites), (2) 7–30 m ($n = 17$), and (3) > 30 m ($n = 9$). The three distance classes were based on (1) the typical crown radius of an adult *Chlorocardium*, (2) one positive standard deviation above the mean nearest-neighbour distance and (3) distances in the second and third deviations from the mean nearest-neighbour value (see Fig. 1A). These classes were considered representative of the different spatial scales at which temporal patterns of incidence in distance-responsive variables might be detected (e.g. Schupp 1992).

The validity of assumptions underlying parametric statistics were evaluated using residual diagnostics generated in the MGLH module of Systat 5.1 (Wilkinson 1989). Transformations of the response and/or predictor variables were employed, based on the Box-Cox method (Weisberg 1985), when the assumptions could not be maintained. Degrees of freedom associated with F -tests of the fitted models compared to the sample sizes (n) stated indicate the extent of outlier rejection.

In cases where response variables could not be fitted into a linear least-squares model, a non-linear, maximum-likelihood estimation procedure was used to fit the predictor variables to logit-trans-

formed data. Since least-squares and maximum-likelihood solutions yield identical results when data are normally distributed (Sokal and Rohlf 1995), the linear-model results are reported here except in the case where normality assumptions could not be met.

Differences in seed attack and germination between paired trunk and crown zones within gaps ($n = 20$) were tested using a t -test for paired comparisons in the Stats module of Systat 5.1. The overall incidence of beetle attack by 85 weeks could not be normalised by transformation. A non-parametric sign test was used to test for differences in this case (Zar 1984).

Results

Incidence of seed attack

Overall, 96% of all seeds artificially dispersed (NT, $n = 480$) were attacked by insects and/or rodents by 85 weeks. Insects attacked 80–90% of all seeds in all treatments ($n = 480$ each) by 85 weeks. This was predominantly due to attack by beetles which accounted for 88, 90 and 78% of all attacks in CI, C and NT groups, respectively. Attack by ants was not more than 6% of seeds in any treatment. Attack in C was greatest, the addition of insecticide in CI resulting in only negligible reductions in overall attack.

Neither distance from nearest reproductive adult nor canopy cover could explain any significant variation in the overall attack incidence by beetles among (C treatment) replicates when fitted into a logit model (Table 1). In contrast, attack on (C treatment) seeds by attine ants was negatively associated with canopy cover, but not significantly influenced by distance (Table 1). Model incorporation of distance and canopy openness explained a fifth of the total variation in the proportion of seeds attacked by ants (Table 1).

The overall incidence of rodent attack (seeds partially or totally consumed at site + seeds removed) on *Chlorocardium* seeds was 43% (NT, pooled $n = 480$). Over 74% of attacked seeds were removed more than 1 m from the implantation site, but only 3% of removed seeds had been partially consumed at the site prior to removal. Less than 1% of attacked seeds were entirely consumed at the implantation sites.

Teethmarks measured on *Chlorocardium* seeds during the fruiting season of 1992 suggested that *Myoprocta* (upper incisor width, mean \pm 1 SD = 1.9 \pm 0.2 cm; $n = 22$) and *Proechimys* (mean \pm 1 SD = 1.2 \pm 0.1 cm; $n = 13$) consumed at most, based on the range of their teeth sizes, 43% and 26% of *Chlorocardium* seeds recorded as being attacked beneath adult trees ($n = 200$ seeds), respectively. *Dasyprocta* (mean \pm 1 SD = 3.1 \pm 0.5 cm; $n = 56$) and *Agouti* (mean \pm 1 SD = 3.4 \pm 0.6 cm; $n = 13$) could account at most for 58% and 29% of damaged seeds, respectively (Fig. 2).

Both distance from nearest reproductive adult and level of canopy cover were poor predictors of the total proportion of seeds attacked by rodents when incorporated into the specified least-squares model (Table 1).

Table 1 Results of multiple-regression analyses of the total number of seeds attacked at 85 weeks and the mean time to attack (MTA) during this period. Attack by insects is assessed based on the C (cage alone) treatment and attack by rodents was based on the NT (no cage, no insecticide) treatment. The independent effects of

distance and openness are presented as standardised beta-coefficients (*b*). The overall model examines the combined variation explained (R^2) by incorporation of distance and openness variables. The difference between *n* and *df* in the overall model denote the extent of statistical outlier rejection

Source	Distance to nearest adult			Canopy openness			Overall model					
	<i>b</i>	<i>t</i>	<i>P</i>	<i>b</i>	<i>t</i>	<i>P</i>	<i>n</i>	R^2	<i>df</i>	<i>F</i>	<i>P</i>	
Cumulative % attacked by:												
Scolytid beetles ^a							40	6.75 ^b	2	2.4 ^c	0.3	
Attine ants	-0.01	0.04	n.s.	-0.46	3.08	0.004	40	0.21	2,35	4.8	0.02	
Rodents	0.13	0.78	n.s.	-0.18	0.5	n.s.	40	0.02	2,37	0.4	n.s.	
MTA by:												
Scolytid beetles	0.65	5.14	<0.001	-0.23	1.8	0.08	38	0.45	2,36	14.1	<0.001	
Rodents	-0.15	-0.9	n.s.	-0.04	0.23	n.s.	38	0.02	2,35	0.4	n.s.	

^a Logit model employed
^b Log likelihood value
^c Chi-squared statistic

Seasonality of seed attack

The mean MTA for all sites calculated for beetles varied considerably between the three treatments, with the NT seeds experiencing attack, on average, nearly 150 days earlier than seeds in the CI treatment group (Fig. 3). The

earliest recorded attack occurred 16 days after implantation of seeds at the sites, while a few seeds remained uninfested beyond 85 weeks.

Distance showed a strong, positive effect on the MTA by beetles in the C treatment set, though canopy openness could not explain any significant portion of the variation in MTA among the sites (Table 1).

The effect of distance on the timing of attack by beetles can also be clearly seen by examining the probability density function of attack times for (C treatment) plots grouped into three distance classes (Fig. 4A). Below parent trees (< 7 m distance), most attack occurred in two relatively early periods in the census, one within 100 days of implantation and another, much broader, peak covering a period of over 6 months from September to March. At sites between 7 and 30 m, three peaks

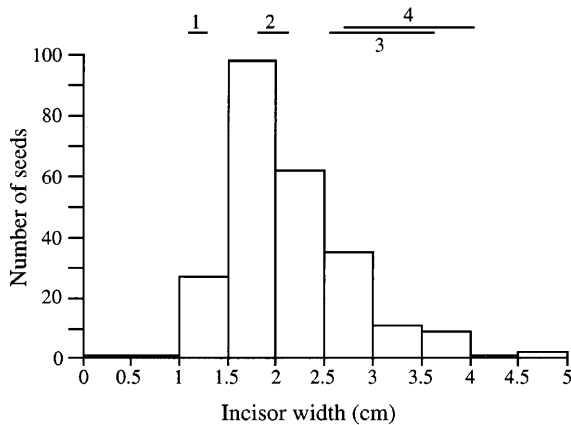


Fig. 2 Distribution of incisor widths taken from *Chlorocardium* seeds (*n* = 200). Horizontal lines at top represent range of incisor widths measured for *Proechimys* (1), *Myoprocta* (2), *Dasyprocta* (3) and *Agouti* (4)

Fig. 3 Box plots of the mean time to attack by scolytid beetles and rodents and mean time to germination (of root and shoot) according to treatment (CI = cage + insecticide, C = cage only, NT = no cage, no insecticide). The top, middle and bottom horizontal lines on the box correspond to the 75th, 50th and 25th percentiles, respectively. The vertical lines extending from the top and bottom of each box represent the 90th and 10th percentiles, respectively. The wide horizontal line extending beyond the vertical edges of each box is the arithmetic mean

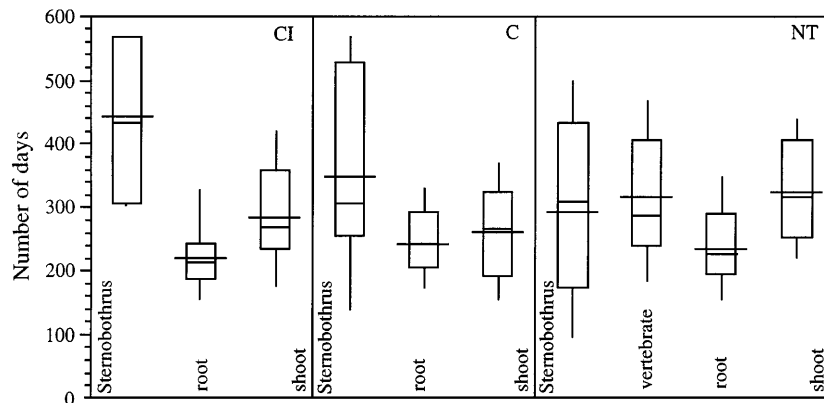
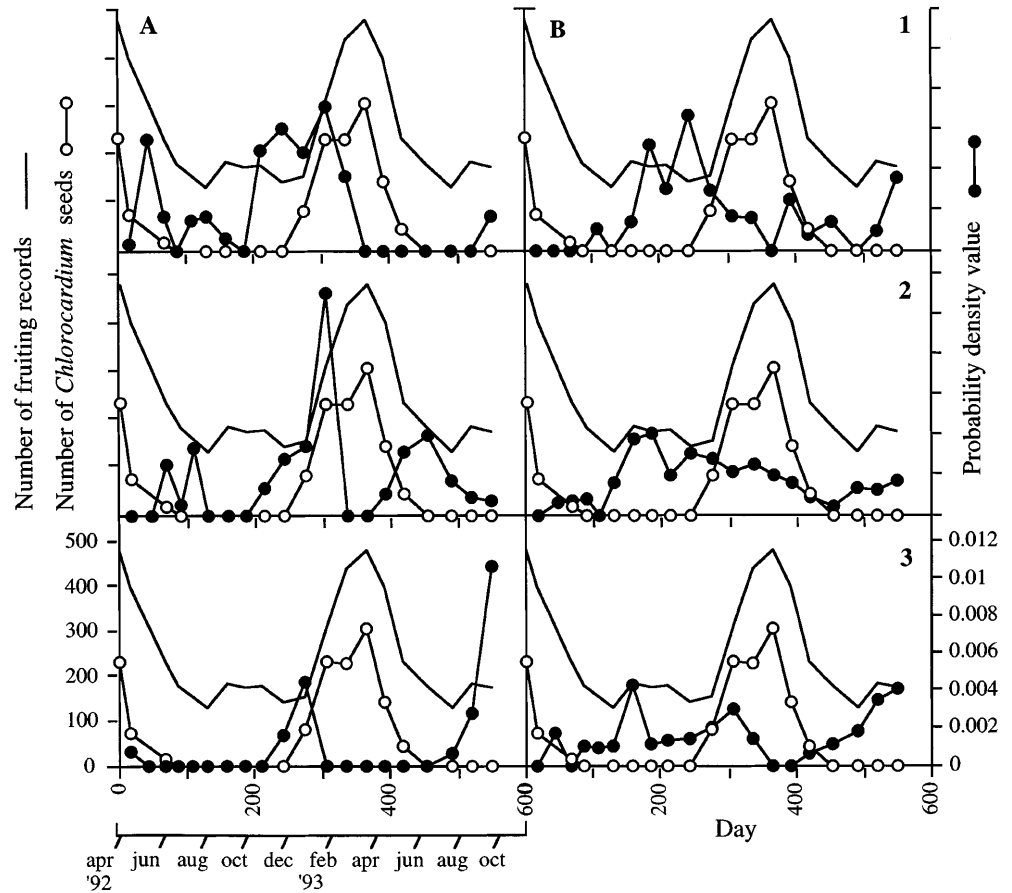


Fig. 4 Probability density function values (filled circles) for Scolytid beetle attack (C treatment) (A) and rodent attack (NT) (B) according to distance intervals of < 7 m (1), 7–30 m (2) and > 30 m (3) from the nearest reproductive *Chlorocardium* adult during the study period. The solid line without symbols represents the total number of expected fruiting trees in the area from a 100-year phenology record (Ter Steege and Persaud 1991) and the open circles represent the actual number of *Chlorocardium* seeds falling during the course of the study at nearby plots



occur, the first two being consistent with the timing of the peaks below trees, and a third occurring in May–June 1993. At distances exceeding 30 m, there was no early peak in the probability of attack. The second peak in December 1992 is small in comparison to the third peak found near the end of the census in October–November 1993.

Seeds were attacked by rodents, on average, sometime during February, 1993, though attacks occurred as early as 44 days and as late as 566 days after implantation (Fig. 3). The amount of variation in rodent MTA explained by distance and canopy openness, as with the model analysis for total proportion of seeds attacked, was small and statistically insignificant (Table 1).

Distance was a good predictor of the degree to which *Chlorocardium* seeds were removed by rodents before or after beetle attack ($n = 40$, $R^2 = 0.43$, $F_{1,38} = 28.1$, $P < 0.001$) (Fig. 5). The greater the distance between the site and the nearest adult tree, the greater the number of uninfested seeds being removed relative to those removed with beetles inside ($b = 0.65$, $t = 5.3$, $P < 0.001$).

The probability of attack by rodents beneath parent trees during the census period showed a strong, early peak from September to January, a period of reduced overall fruit availability (Fig. 4B). The timing of this peak is maintained at larger distance intervals, though a second peak during the same period in the subsequent

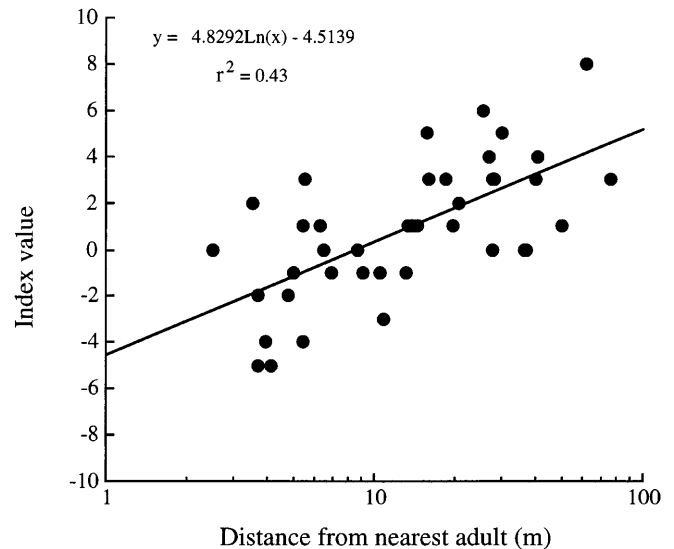


Fig. 5 The effect of distance from nearest reproductive *Chlorocardium* on the likelihood of seeds being removed by rodents before (+) or after (–) *Sternobothrus* colonization. A positive (+) value indicates that more seeds at a site were removed by rodents prior to infestation whereas a negative (–) value indicates the reverse. The degree of discrepancy between rodent and *Sternobothrus* attack times is indicated by the size of the value

year was more pronounced at distances > 30 m from parent trees than at shorter distance intervals.

Germination success and timing

Over 60% of all seeds (pooled $n = 480$) in the NT treatment formed a root radicle by 85 weeks. An additional 10% of seeds reached this stage of germination in the C treatment, with the application of insecticide (CI) yielding a negligible increase (73%). Subsequent shoot formation occurred in 83%, 79% and 84% of rooted individuals in NT, C and CI treatments, respectively.

Neither distance nor canopy openness were good predictors of root radicle formation success in CI or NT (Table 2). Distance explained 58% of the variation in root radicle formation, after accounting for canopy openness effects, when vertebrates were excluded without insecticide treatment (C). However, distance did show a strong positive correlation with germination success when the proportion of individuals successfully forming a shoot in CI and C was analysed, though canopy openness did not (Table 2).

The onset of root radicle formation occurred as early as 55 days following implantation and as late as 381 days in some seeds, though several individuals germinated long after the final date reported here. The mean MTG for root radicle formation in all plots did not vary by more than 24 days among the three treatments, while the mean MTG for shoot extension varied no more than 41 days among the treatments (Fig. 3).

When incorporating MTG for each site into a model with canopy openness and distance from parent as

predictor variables, there was no significant relationship when considering time to root radicle formation, but a highly significant, positive relationship between the MTG for shoot extension and the distance from nearest adult *Chlorocardium* was evident (Table 2). The effect of distance and canopy openness was similar for seeds in the C treatment, but not in the NT treatment (Table 2).

The spread of $f(t)$ values for each census period suggests a bimodal distribution in germination, with a major peak in root radicle initiation during the transition to a high-rainfall period in May–June 1992 and a subsequent minor peak in February 1993. These peaks in probability were similarly positioned at all distance classes (Fig. 6A). The peak probability of epicotyl initiation below adult trees occurred immediately following the peak in root radicle formation (Fig. 6B). However, at greater distances, an early peak in shoot initiation did not occur. There was no clear peak probability of shoot initiation at distances between 7 and 30 m. In contrast, the highest probability of shoot initiation occurred immediately after the second peak in root radicle formation at distances beyond 30 m (Fig. 6B).

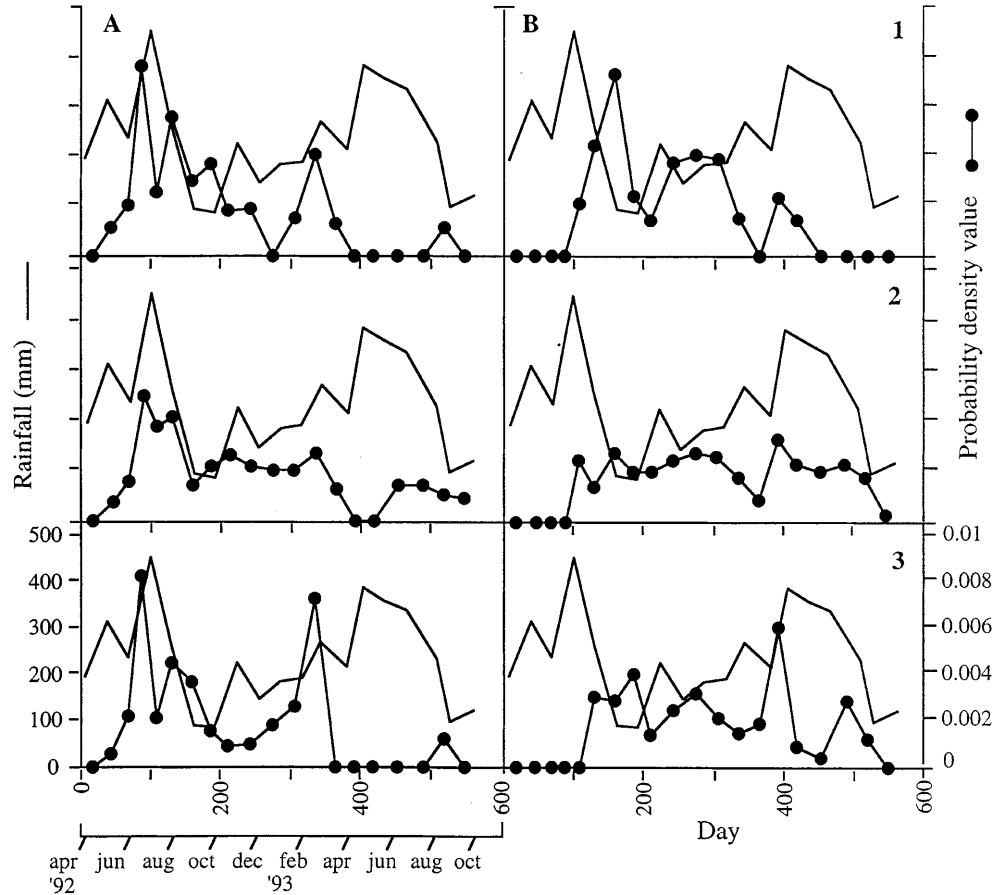
How important was the effect of distance on the timing of beetle attack in relation to germination success? If beetle attack reduced the likelihood of shoot formation, then an increased ‘window’ of time prior to attack should enable a larger number of individuals at each site to reach the shoot-forming stage. This was clearly the case, with over half of the variation in the $(\log + 1)$ -transformed number of seeds germinating prior to attack by beetles (weighted by overall germination success in the set of eight seeds in C) being significantly

Table 2 Results of multiple-regression analyses used to examine the effects of distance and openness on cumulative germination success at 85 weeks and the mean time to germination (MTG) during this period. Germination assessment is based on the formation of a root and shoot in each of three treatments: CI cage+insecticide, C cage alone, NT no cage, no insecticide.

The independent effects of distance and openness are presented as standardised beta coefficients (b). The overall model examines the combined variation explained (R^2) by incorporation of distance and openness variables. The difference between n and df in the overall model denote the extent of statistical outlier rejection

Source	Distance to nearest adult			Canopy openness			Overall model				
	b	t	P	b	t	P	n	R^2	df	F	P
Cumulative % forming:											
Root radicle											
CI	0.1	1.7	n.s.	0.01	0.61	n.s.	40	0.08	2,36	1.7	n.s.
C	0.57	4.28	<0.001	0.17	1.25	n.s.	40	0.35	2,37	9.98	<0.001
NT	-0.25	1.56	0.13	0.15	0.94	n.s.	40	0.08	2,37	1.7	n.s.
Shoot											
CI	0.45	3.1	0.004	-0.15	1	n.s.	40	0.02	2,36	5	0.01
C	0.64	5.1	<0.001	0.08	0.61	n.s.	40	0.42	2,37	13.4	<0.001
NT	0.15	0.89	n.s.	-0.01	0.07	n.s.	40	0.02	2,37	0.4	n.s.
MTG for:											
Root formation											
CI	0.11	0.69	n.s.	0.01	0.03	n.s.	40	0.01	2,37	0.24	n.s.
C	-0.07	0.42	n.s.	0.17	1.07	n.s.	40	0.03	2,37	0.66	n.s.
NT	-0.22	1.39	n.s.	0.04	0.22	n.s.	40	0.05	2,37	0.99	n.s.
Shoot formation											
CI	0.56	4.2	<0.001	-0.16	1.19	n.s.	40	0.35	2,37	9.95	0.001
C	0.43	2.9	0.01	-0.13	0.86	n.s.	40	0.2	2,36	2.36	0.02
NT	0.25	1.49	0.15	-0.17	0.98	n.s.	35	0.09	2,32	1.6	n.s.

Fig. 6 Probability density function values (filled circles) for root radicle formation (A) and shoot formation (C treatment) (B) according to distance intervals of <7 m (1), 7–30 m (2) and >30 m (3) from the nearest reproductive *Chlorocardium* adult during the study period. Monthly rainfall for the study period was measured 1.5 km from the study plot



explained by distance ($n = 40, R^2 = 0.53, F_{1,38} = 42.3, P < 0.001$) (Fig. 7).

Trunk versus crown zones in gaps

No differences in the overall incidence of attack by beetles (C), attine ants (C), or rodents (NT) between

sites were detected, though the probability of detecting a true difference in attack by rodents between paired samples was only marginally less than the critical α -level (mean \pm SD difference = $11.8 \pm 26.9; t = 1.96, df = 19, P = 0.055$). There were no differences in the overall proportion of seeds forming a root radicle or a shoot between zones. Differences in the MTA (C, NT) and MTG (CI, C, NT) by rodents and insects also showed no significant differences between zones.

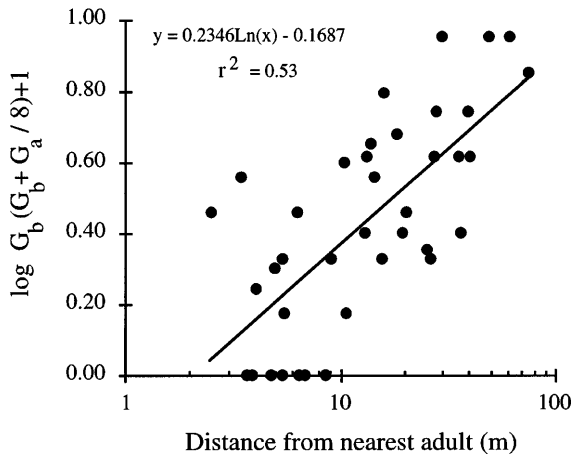


Fig. 7 Regression between the number of uninfested *Chlorocardium* seeds forming a shoot and distance from nearest conspecific adult. Uninfested seeds (G_b) were weighted by the overall fraction of seed-forming shoots [$G_b +$ infested (G_a)] at each site and log transformed

Discussion

Seedfall in *Chlorocardium* appears to be a regular, (semi-)annual event (Zagt 1997). Though not all individual trees reproduce consistently every year, the highly aggregated distribution of adults appears to buffer the drastic year-to-year variation in per capita output which can lead to a less predictable pattern of seed availability in many other Guianan tree species (e.g. Forget 1997). In addition, predispersal predation of fruit is typically low (Ter Steege et al. 1996). This creates a ‘patch’ of relative high seed density which, combined with a large seed size and extraordinarily protracted germination within a cohort (see Fig. 4), lends a spatial and temporal predictability to *Chlorocardium* seeds shared by few other sympatric tree species (D.S. Hammond, personal observation).

Consumers and colonisers of *Chlorocardium* seeds

Despite substantial alkaloid defences (bibirine – a curare analogue; see Ter Steege 1990), which were thought to preclude predation on *Chlorocardium* (Janzen 1974), nearly half of all *Chlorocardium* seeds were attacked by rodents. The highest likelihood of attack occurred consistently during expected periods of low fruitfall, regardless of distance from the nearest parent tree. As fruitfall increases, a substantial decline in the probability of attack ensues, suggesting that *Chlorocardium* does not occupy a high position in the hierarchy of rodent resource selection, but spans the gap between consecutive peaks in the availability of more attractive resources. Based on toothmark matching, *Dasyprocta* and *Myoprocta* are the main consumers of *Chlorocardium*, though it is unknown if seasonal partitioning in seed use occurs between these species and the other putative consumers. However, *Dasyprocta* and *Myoprocta* are considered to restrict their diet to hard seeds more than any other tropical rainforest rodents (Smythe 1986; Henry 1994), principally by scatter-hoarding seeds across their home ranges. The lack of any significant effect of distance on the frequency of rodent attack upon *Chlorocardium* further supports the view that vertebrates forage throughout their home ranges and do not respond to a gradient of declining seed density with distance from the parent tree (see Hammond and Brown 1998). Recruitment success may not be as sensitive to dispersal distance as previously believed (Janzen 1970), but can be more strongly influenced by frequency-dependent selection processes (Greenwood 1985) and spatial patterns of habitat use by seed-eaters.

Resource quality can have an important effect on brood size of scolytids (e.g. Beaver 1979) and seeds of *Chlorocardium* typically contain high levels of starch (see Ter Steege 1990). However, it is uncertain whether, in this case, it is the energy content or the suitability of the seed mass as a substrate for fungi which determines if *Chlorocardium* is a superior resource for scolytid beetles, given that fungi have been observed in the parental galleries within seeds (D. Hammond, personal observation), and many neotropical, stem-boring species of *Sternobothrus* are known to be mycetophagous, at least as adults (Beaver 1973). Brood sizes of *Sternobothrus* in *Chlorocardium* seeds under one adult tree ranged from 8 to 83 offspring ($n = 78$ seeds), which is not atypical of accounts for other colonising scolytid and host plant species pairings (Kirkendall 1993).

Spatial concordance: disturbance and dispersal distance

Neither germination, rodent attack nor beetle attack were significantly affected by the range of canopy openness conditions examined here. Like canopy openness, the distance between replicate site and nearest adult *Chlorocardium* was not a significant predictor of the final proportion of seeds attacked in the cohort by

either rodents or insects, or the fraction of seeds forming a root radicle. Distances between implanted seeds and nearest reproductive adult ranged from 2 to 76 m. Though most seeds are found within 7 m of adult trees, dispersal down steep slopes, which typically accommodate high densities of *Chlorocardium* trees (Fanshawe 1954), and by surface flow during unusually heavy rainstorms can move seeds up to 30 m from the parent tree (D. Hammond, personal observation). The fate of the majority of seeds removed by rodents in the experiment is unknown, but single *Chlorocardium* seeds have been found partially consumed as far away as 50 m from the nearest adult in the study plot. Since it is unlikely that dispersal of *Chlorocardium* seeds away from adult conspecifics would exceed the maximum distance tested in our experiment, it is reasonable to state that dispersal does not decrease the likelihood of attack at 85 weeks after release.

This suggests that the main spatial gradients, viz. canopy openness and distance from adult, which might lead to differences in germination or attack at the study site, in fact have no effect when holding time constant (up to 85 weeks). The overall impression is one of a species capable of germinating at any location in the habitat, but one attacked by rodents and insects equally across the entire habitat area.

Temporal discordance: the phenology of attack, dispersal and germination

Though the cumulative fraction of seeds attacked or forming a root radicle was insensitive to distance from nearest adult *Chlorocardium*, the temporal distribution which led to these outcomes was far more responsive to this variation. The MTA by beetles was strongly affected by distance from the parent tree, with most seeds beneath trees being attacked early and the MTA increasing with distance. Distance could not explain any variation in the MTA by rodents, but was a good predictor of the degree to which *Chlorocardium* seeds were removed by rodents both before and after beetle attack. Interestingly, both the total fraction of individuals forming a shoot at 85 weeks and the MTG for shoot formation were strongly associated with distance to the nearest adult tree in treatments excluding rodents (CI and C), but not in the control group (NT). The effect of distance on shoot formation may not have been detected in the NT group due to rodent removal of seeds without regard to prior beetle infestation.

The peak probabilities of root formation (Fig. 6A) and beetle attack (Fig. 4A) suggest that a larger proportion of seeds are attacked during the main peak in root radicle formation beneath *Chlorocardium* trees. At further distances, the main peak in attack occurs well after most seeds have already formed a root. Given that beetle colonisation is likely to be followed by fungal invasion (D. Hammond, unpublished data) and, as a consequence, seed mortality, it is clear that the timing of

colonisation, which is sensitive to distance, decouples the concordant relationship between the root formation response of *Chlorocardium* and the spatial characteristics of the habitat. The outcome of this discordance between the temporal pattern of attack and distance is expressed by the significant effects of distance on both the total fraction of individuals forming a shoot and the MTG of shoot formation (Table 2). Below parent trees, seeds which root early are less likely to succumb to the ill-effects of beetle colonisation and produce an early peak in the probability of shoot formation compared to seeds which fail to root or root later but die soon thereafter. This is reflected in the strong positive effect of increased distance on the number of individuals forming a shoot prior to infestation (Fig. 7). At greater distances, the peak probability density of shoot formation is less pronounced, being more evenly spread throughout the study period (Fig. 6B), due to the reduced probability of attack in the first 250 days following implantation (Fig. 4A).

The probability of rodent attack on seeds was independent of distance, but negatively associated with the expected overall resource availability at the site (Fig. 4B). However, due to the much shorter MTA by beetles beneath adult trees, there was a significant decline in the number of uninfested seeds removed at shorter distances from the nearest reproductive adult. This suggests that the putative dispersal by rodents may be ineffective as a mode of escaping beetle-induced mortality at the site, unless dispersal is succeeding previous dispersal away from the tree (cf. phase II dispersal: Chambers and MacMahon 1994). The likelihood of establishment of the few seeds removed from beneath the tree at an early stage, and which are thus likely to be free of scolytids, still depends on germination taking place prior to beetle colonisation at greater distances and/or subsequent consumption by rodents. *Chlorocardium* adults which release their fruits far past the population and community-level peaks in fruitfall (Fig. 4) should give their offspring a considerable advantage, given that the likelihood of seed removal by rodents beneath trees increases considerably as overall fruitfall declines.

The suppression of shoot formation success (Fig. 6B) by the timing of beetle attack (Fig. 4A) would suggest that initial seedling abundance is partially the product of the number of seeds which can germinate prior to infestation or rodent attack. Near *Chlorocardium* trees, this occurs over a relatively narrow band of time but expands to approximately 250 days at distances greater than 30 m from the nearest adult. Thus, the advantages accrued by dispersal are framed by an 'escape window' that is measured in increments of time and space for *Chlorocardium*, rather than by space alone.

Conclusions

Our study of *Chlorocardium* suggests that the 'race' between mean time to attack and mean time to germina-

tion along spatial gradients may be more important in determining dispersal advantage than distance alone. Based on the results presented here, we would predict that the advantages to dispersal will decline as the germination rate decreases and the attack rate increases. Factors which explain variation in germination and attack rates, such as rainfall and background fruitfall, are indirectly influencing dispersal advantage in *Chlorocardium*. Examining the interaction between dispersal distance, germination and attack rates in other species with contrasting seed attributes may provide a better understanding of how dispersal can influence the population dynamics of tropical trees.

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