# Germination and Growth of Colonizing Species in Artificial Gaps of Different Sizes in Dipterocarp Rain Forest

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# Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest

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## SUMMARY

Population dynamics and height growth of colonizing seedlings were monitored for three years in newly created artificial gaps and beneath intact canopy in primary lowland rain forest in Sabah, Malaysia. The effects of gap size, soil surface conditions and competition from advance regeneration were assessed. Recruitment during the first two years was less than 100 seedlings $m^{-2}$, or less than 5% of the estimated seed bank in the top 5 cm of the soil prior to disturbance. Overall, germination was not obviously affected by gap size, but was increased markedly by soil exposure or disturbance. The diversity of the colonizing vegetation at the end of two years appeared to be negatively related to gap size. Seedling mortality was less both at larger gap size and in the absence of competition from advance regeneration, whereas the opposite appeared true for seedling growth. The results indicate that gap size is unlikely to influence the composition of colonizing vegetation by controlling seed germination, but an effect operating through differential mortality cannot be discounted.

## 1. INTRODUCTION

Studies of tropical rain forest dynamics have for some time recognized the importance of gaps in the canopy, typically the result of treefalls, to the processes of forest regeneration (Jones 1956; Brokaw 1985, 1987; Hubbell & Foster 1986; Denslow *et al.* 1990). The environmental conditions in these unpredictable, transient habitats often differ markedly from those in undisturbed forest (Schulz 1960; Chazdon & Fetcher 1984; Ghuman & Lal 1987; Brown 1990; Kennedy 1991). Although the establishment and growth of many rain forest species benefit from such conditions (Whitmore 1978; Augspurger 1984; Popma & Bongers 1988; Denslow *et al.* 1990), variation among species in the degree of dependence upon gaps has been offered as one explanation for high tree-species diversity in tropical rain forests (Orians 1982; Denslow 1987). Swaine & Whitmore (1988) proposed that, on the basis of seed germination requirements, two ecological groups of tree species can be distinguished: non-pioneer (or climax) species, with seeds which can germinate under a forest canopy, and pioneer species, with seeds which can only germinate if exposed to full sunlight for part of the day. Other authors, however, have reported differential germination (Raich & Gong 1990) or establishment success (Brokaw 1987) of different 'pioneer' species in canopy gaps of different sizes. Some investigations also have revealed apparent differences in the regeneration of pioneer species in different parts of gaps, with some species establishing better than others in particular microsite conditions (Putz 1983; Brandani *et al.* 1988).

Unlike regeneration on rain forest sites after cultivation (Wyatt-Smith 1955; Kellman 1970; Uhl *et al.* 1988) or after clear-felling (Symington 1933; Riswan 1982; Swaine & Hall 1983; Saulei 1985), regeneration in natural treefall gaps has been investigated only recently (Putz 1983; Brokaw 1985, 1987; Hubbell & Foster 1986; Brandani *et al.* 1988; Nunez-Farfan & Dirzo 1988; Uhl *et al.* 1988). Most studies of this type have been based on a single observation in each of several gaps of various estimated ages, and successional changes have been inferred on the assumption that time since disturbance is the overriding factor. Only occasionally (e.g. Brokaw 1987; Uhl *et al.* 1988) have repeated observations been made in the same gaps. Furthermore, because of the problem of locating suitable gaps immediately after their formation, very few studies (e.g. Brokaw 1985) have examined the processes occurring within the first one or two years after gap formation. Similar problems hinder the understanding of the effects of gap size on regeneration in natural gaps but, despite its advantages, the simulation of natural gaps by controlled felling of canopy trees has only rarely been practised (e.g. Uhl, *et al.* 1988). This technique allows gap size to be controlled to some extent, permits monitoring before, and from the moment of, gap creation and facilitates the establishment, within each gap, of different microsite treatments.

This paper describes a study in Sabah, Malaysia, in

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which the early stages of regeneration following disturbance were investigated in artificially created gaps with the aim of determining whether the colonizing species demonstrated any differences in germination, establishment success or growth in gaps of different size or on different microsites within the gaps.

## 2. METHODS

### (*a*) *Gap creation*

The location and general environmental conditions of the study area, in the Danum Valley Conservation Area, Sabah, Malaysia, are described by Marsh & Greer (this symposium).

Five artificial gaps were created in early 1987 by felling trees in mature forest on a gentle ridge running east towards the Segama River at about 250 m altitude (figure 1). Sites for gap creation within the study area were chosen where dipterocarp seedlings required for a companion study (see Brown & Whitmore, this symposium; Brown 1990) were locally abundant. Two small additional gaps (11 and 12) were created in early 1988 because the results from the original gaps suggested that any critical gap size for germination would be very small. Preparing the gaps for experimental purposes was a compromise between simulating natural tree fall and providing homogenous conditions: all woody plants greater than 2 m tall, except dipterocarp saplings, were cut and removed from the felled area. The required range of gaps was achieved mostly by the removal of small trees, although a few large dipterocarps were felled in the largest gaps. In addition, three sites (A, B, C) were established within closed capopy forest to act as control samples (figure 1).

The sizes of the gaps created were subsequently assessed by various structural and microclimatic measurements (Whitmore *et al.* 1992) of which one, % canopy openness, is here used throughout as the measure of gap size.

### (*b*) *Monitoring seedling populations*

In all gaps except gap 3 (figure 1), sample plots were established to monitor the germination and growth of new seedlings. Each plot was inspected in detail on several occasions (for details, see Kennedy (1991)) for newly germinated seeds. These were marked by numbered metal tags, and their positions were plotted on a map to assist in their relocation at a later date. In this way, new recruits could be distinguished from existing seedlings, and any deaths of earlier recruits could be detected. After 8–9 months, the heights of all seedlings that were at least 10 cm tall were also recorded. In July 1990, when many seedlings were taller than 5 m, all woody plants with a girth at breast height (1.3 m) of at least 10 cm were labelled with an aluminium tag embossed with a unique number. Early height measurements were obtained with a 1 m rule; subsequently, an 8 m telescopic measuring pole (SK Senshin) was used.

Two supplementary plots were established in the largest gap, gap 4, six months after gap creation, to provide a larger sample area. In these plots, growth and mortality of seedlings present when the plots were established were monitored, but germination was not assessed.

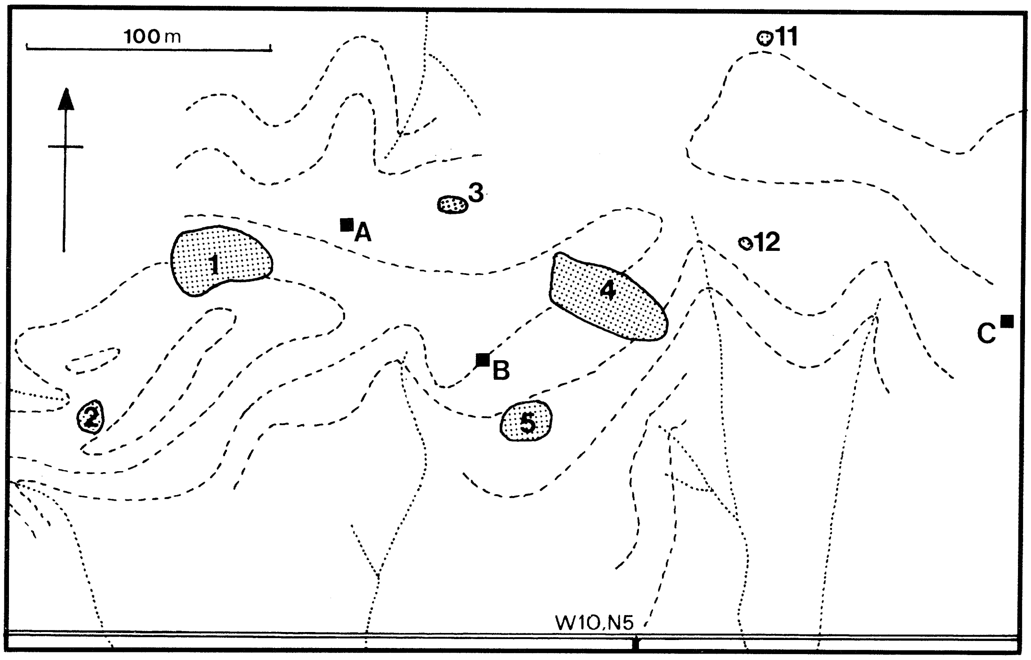

Figure 1. Map of study area, showing relative positions of artificial gaps and closed forest control sites. Stippled areas indicate approximate extents of canopy gaps. Broken lines are approximate contours at 5 m intervals above the W10,N5 (bottom centre) intersection of the Danum Valley Field Centre research trail grid. Dotted lines represent approximate stream courses.

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Identification of seedlings was difficult, as all were immature, and few taxa were well-known trees. Recognizably distinct taxa were initially recorded using code names, which were subsequently converted to scientific names by comparing specimens in herbaria (Sabah Forest Department, Sepilok; Forest Research Institute Malaysia, Kepong; Royal Botanic Gardens, Edinburgh), and by consulting relevant texts (Backer & van den Brink 1963, 1965; Keng 1969; Whitmore 1972, 1973; Cockburn 1976, 1980; Ng 1979; Vogel 1980; Corner 1988) and Dr M. van Balgooy of the Rijksherbarium, Leiden.

### (*c*) *Soil surface treatments*

Three soil surface treatments were applied to test their effect on seed germination after gap creation. These were: (i) undisturbed soil surface (U); (ii) surface leaf litter removed (E); and (iii) surface leaf litter removed and soil scarified to about 5 cm deep with a hoe (S). Treatments E and S are collectively referred to as disturbed soil. Because of limited space in the smaller gaps, not all soil surface treatments could be applied in all gaps. All three treatments were, however, effectively applied across the full range of gap sizes, including the closed forest control sites. Most plots were established in March–April 1987, the controls in July 1987, and those in gaps 11 and 12 in March 1988. Consequently, the periods over which regrowth was monitored varied among the gaps, but all samples were assessed frequently for at least one year. The supplementary plots in gap 4 both received the undisturbed soil treatment.

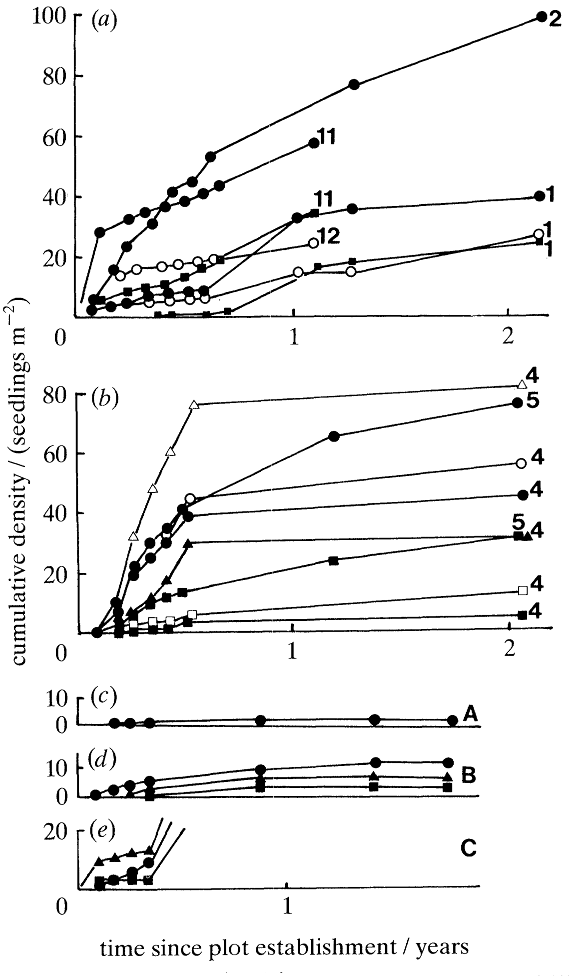

Figure 2. Cumulative germination in sample plots: (*a*) and (*b*) artificial gaps, (*c*)–(*e*) closed forest control sites. Location of each plot indicated by gap number or letter designating control site. Solid symbols represent the treatment with competition; open symbols, without competition; circles = scarified-soil, triangles = exposed-soil, squares = undisturbed-soil treatments.

### (*d*) *Competition treatments*

Soon after gap creation, it became clear that resprouting from cut stumps and growth of other plants that survived gap clearance would be substantial, especially in the larger gaps. To assess the effects of this on new seedlings, the plots were divided into two competition treatments: (i) without competition (−): plants of non-study species removed and resprouts periodically cut back; (ii) with competition (+): surviving plants and post-gap resprouts allowed to grow.

The treatment without competition was first applied to parts of gaps 1 and 4 (including one supplementary plot) approximately six months after gap creation, and reapplied roughly every month for the next 18 months. In gap 12, it was applied for approximately the first year after gap clearance.

In July 1987, a survey of resprouting of cut stumps was conducted in three gaps (gaps 3, 4 and 5) with canopy openness values of 6, 13 and 30%, respectively. In gap 3, all stumps were sampled (51), but in gaps 4 and 5, random samples were taken (81 and 108 stumps, respectively). Stump height, diameter, number of shoots and length of longest shoot were recorded.

## 3. RESULTS

### (*a*) *Germination*

The progress of seed germination in the various sample plots is shown in figure 2. Most samples show rapid initial rates, with subsequent decline, although there is substantial variation among samples. Particularly evident is the extended period over which germination continued: in many plots the initial period of rapid appearance of new seedlings continued for 200 days. Although the rate of germination typically declined in the second year after gap creation, it was often substantial; notably in gap 2, a small gap (canopy openness 8%), in which the rate for the final 1.5 years to April 1989 averaged 28.6 seedlings m$^{-2}$ y$^{-1}$, compared with 87.6 m$^{-2}$ y$^{-1}$ over the first 225 days (0.6 years). By any standards this must be regarded as an unusually protracted period for germination from a single disturbance.

Excluded from figure 2 are 404 seeds of one unknown species in the Rubiaceae which germinated between 125 and 350 days in all three soil surface treatments in the closed forest (control) sample C (Appendix). Apart from these, only a total of nine

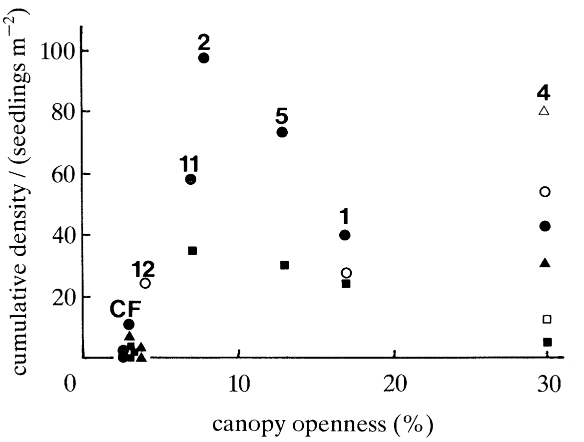

Figure 3. Cumulative germination by April 1989 in gaps of different size. Sample plots are indicated by gap numbers above symbols. All closed forest sites (CF) were assigned canopy openness value of 3%. Key to symbols as in figure 2.

seeds germinated in the three closed forest samples (Appendix).

The accumulated numbers of seeds which had germinated by the end of the initial study period in April 1989 are plotted against gap size in figure 3. Apart from very low numbers of seedlings in closed forest control plots (excluding those described above), there is no clear relationship between gap size and amount of germination: variation within most gaps was at least as great as between gaps. Even the smallest artificial gaps, 11 (7% openness) and 12 (4% openness), have numbers of seedlings within the range for the largest gap, 4 (30% openness).

Compared with the estimated number of germinable seeds in soil samples taken prior to gap creation (Kennedy 1991), those germinating in the gaps represented a very small proportion of the available soil seed bank. Expressed as a percentage of the soil seed bank density in the top 5 cm at each gap site, the average germinating over two years after gap creation was only 2.3%, with a range of 0.2–4.5%.

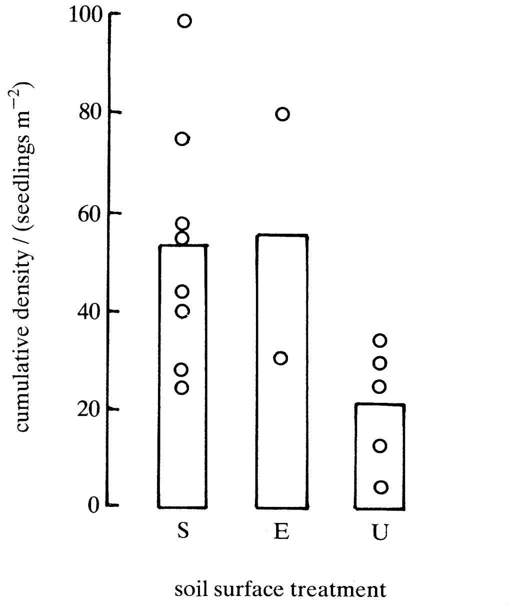

Figure 4. Cumulative germination by April 1989 in different soil surface treatments. Open circles represent totals for individual plots, columns represent treatment means.

Soil surface treatment had marked effects on the number of seeds germinating (figure 4). Scarification resulted in 2.5 times as many seedlings, on average, as the undisturbed (litter-covered) soil. The exposed treatment, with only two samples, produced widely different results, but with an average similar to the scarified treatment. The closed forest samples are excluded from figure 4, but showed a similar ranking of seedling numbers with soil surface treatment (figure 2 *c–e*). Comparisons of cumulative germination between scarified and undisturbed treatment in the same gaps were made using paired *t*-tests. Differences were significant for the data at three months after the treatments were established ($t = 4.67$, $n = 5$, $p < 0.01$), at six months ($t = 5.13$, $n = 5$, $p < 0.01$) and in April 1989 (figure 4; $t = 5.83$, $n = 5$, $p < 0.005$). Similar tests for the closed forest samples gave no significant differences between treatments because of the very small numbers of seedlings in these samples.

### (*b*) *Composition of seedling regeneration*

Relatively few taxa were common to all gap sizes (Appendix), and specific comparisons are, therefore, of little value. Comparisons of life-form spectra are more informative. There is considerable variation among gaps in the proportions of the seedlings in different life-form categories, but there is no consistent trend with gap size (Kennedy 1991). Much of this variation is due to large numbers of seedlings of single taxa in some gaps. When based on the number of taxa the contributions of the life-forms are much more uniform among gaps. Trees and scandent shrubs predominate (on average 33.5% of taxa respectively), followed by erect shrubs (11.9%). About 15% of taxa were unidentified. Bole climbers (4.5%) and herbs (2.4%) are generally uncommon. These data suggest that gap size does not exert any selective influence on life-form representation in gap regrowth.

The rate of acquisition of new taxa generally follows the pattern of seedling recruitment (figure 2). Neither gap size nor the influence of competing vegetation had any effect on the total number of taxa appearing as seedlings. However, as measured by the Shannon-Weiner index (H′), which incorporates both the number of taxa and their abundance, the diversity of the seedlings surviving in April 1989 showed a decline with increasing gap size (figure 5), caused principally by decreasing evenness of representation amongst the species. The results also suggest that, in April 1989, samples on disturbed soil had generally higher diversity than those on undisturbed soil, and that competition with other vegetation enhances colonizing seedling diversity (figure 5).

Ordination (Detrended Correspondence Analysis, Hill & Gauch 1980) of seedling composition amongst gaps revealed no clear relationship with gap size

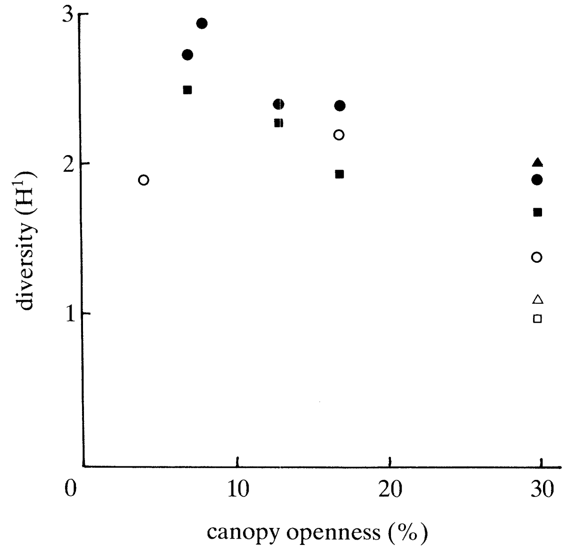

Figure 5. Shannon-Weiner indices of diversity for colonizing vegetation established in gaps of different size in April 1989. Key to symbols as figure 2.

(Kennedy 1991, figure 8.9). Although the two smallest gaps were separated from the remainder, these two (gaps 11 and 12) were established approximately one year later than the others. Furthermore, much of the difference in composition was attributable to the occurrence of several species whose distributions were confined to single gap sites (Appendix) and probably reflect differences in pre-gap soil seed bank composition rather than differences in gap environment.

### (*c*) *Seedling mortality*

Mortality of seedlings in the gap samples has many causes which cannot be identified with certainty. Two phases of mortality may, however, be recognized. Initial mortality is relatively high, caused by microsite effects on very small seedlings, such as desiccation or predation by small terrestrial animals. For larger seedlings, competition with other seedlings is important, and will continue as the new plants become larger. In the samples where the advance regeneration was not cut back, this too will add its influence.

The earliest mortality is the most difficult to assess because it may occur very rapidly, usually before the seedling can be assigned to a taxon and perhaps even before the germinating seedling emerges above ground. An unknown number of seedlings may thus have germinated and died in the 4 weeks between successive initial enumerations and perhaps in the longer intervals between enumerations in the second year. Figure 6 shows survivorship of three representative seedling cohorts, plotted on a logarithmic scale in which constant mortality appears as a straight line. For most samples (e.g. cohort 3 in figure 6), mortality was initially higher, due to the deaths of young, very small seedlings.

Subsequent mortality (after the second enumeration of each cohort) can be reasonably represented by a linear regression, the slope of which is used here as the measure of each cohort's mortality rate. There is a striking difference in mortality between cohorts of the same age growing in Gap 4 and without competition from advance regeneration. The data (figure 7) show that all except two of the cohort pairs have higher mortality with competition than without. This effect is greater amongst cohorts which germinated later because the seedlings which germinated earlier are better able to keep pace with the resprouts. In other gaps, however, where the competing regrowth was less well-developed, differences between the treatments with and without competition were not consistent (figure 8).

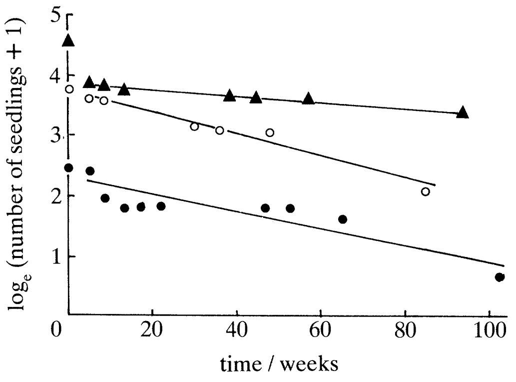

Figure 6. Survivorship curves for three cohorts of seedlings which germinated in the scarified-soil treatment with competition in gap 4. The cohorts shown germinated in the first (solid circles), third (solid triangles) and fifth (open circles) months after gap creation.

In the plots with competition in the largest gap, 4, soil surface treatment has a marked effect on seedling mortality, with higher rates amongst disturbed soil treatments (scarified and exposed) than undisturbed (figure 7). Mortality was generally higher amongst cohorts which germinated later compared with the early cohorts, presumably because late germinants have to compete with seedlings and regrowth established earlier. The lower mortality rates in undisturbed soil may be the result of lower seedling density in these samples (see figure 2*b*). The results of similar comparisons within other gaps are equivocal, perhaps because the effects of other factors, such as solar radiation levels, increasingly obscure those of soil surface treatment as gap size declines.

Seedling mortality is also related to gap size, with seedlings in larger gaps suffering less mortality (figure 8). This correlation is significant for all soil surface treatments (table 1), and appears to hold for both competition treatments. The reasons for declining mortality with increasing gap size are probably related to the increase in incident solar radiation. Larger gaps develop dense vegetation more quickly, however, and the increasing competition might be expected to result in higher mortality. The very low rates of mortality in the closed forest samples may be due to low seedling density and because the few germinating seeds may have belonged to shade-tolerant (non-pioneer) species.

None of the species germinating in the plots was

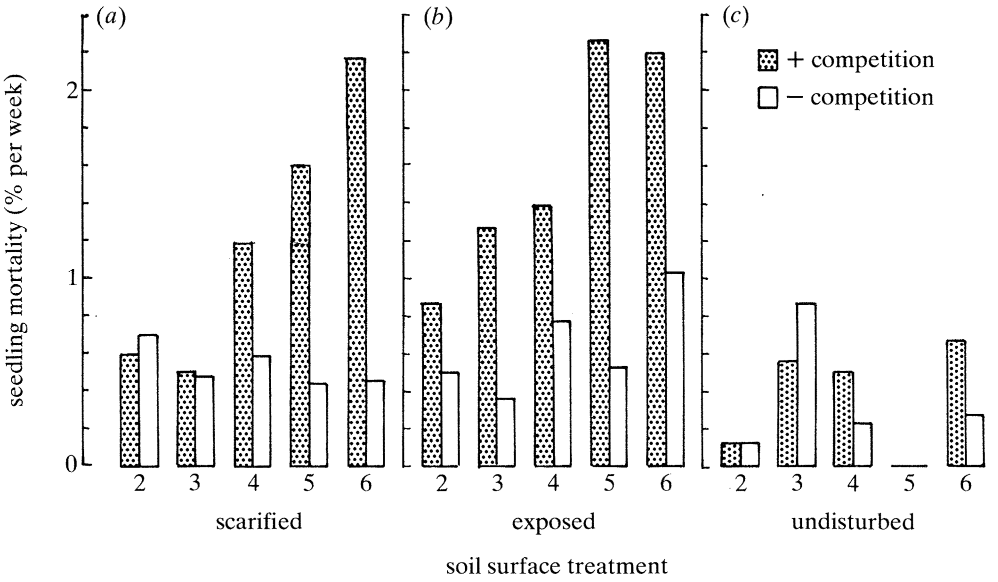

Figure 7. Instantaneous mortality rates of individual monthly cohorts of seedlings which germinated in the experimental plots in gap 4 in (*a*) scarified, (*b*) exposed and (*c*) undisturbed soil treatments. Numbers along bottom of the figure indicate the months in which the cohorts germinated.

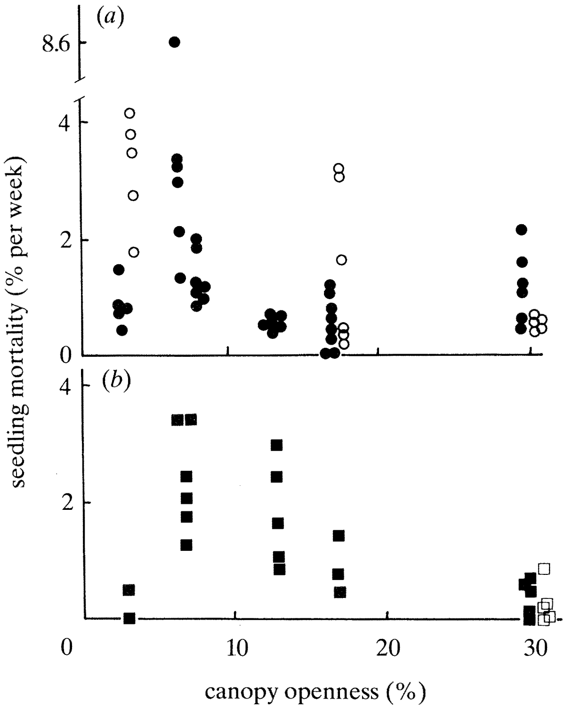

Figure 8. Instantaneous mortality rates of individual cohorts of seedlings recruited within the first 8 months after gap creation plotted against canopy openness. (*a*) Scarified-soil treatment, (*b*) undisturbed-soil treatment. Open symbols, without competition; closed symbols with competition.

sufficiently widespread to test for differences in mortality rate between species in relation to gap size.

### (*d*) *Seedling height growth*

Height growth in the first year after gap creation was generally relatively slow: few leading plants were greater than 2 m tall at the end of the first year.

Table 1. *Correlation coefficients between seedling cohort mortality and gap size, as measured by % canopy openness, for samples from different soil surface treatments. Only plots with competition are included*

| treatment group | correlation coefficient | d.f. | *p* |
|---|---|---|---|
| scarified soil | −0.440 | 48 | <0.01 |
| undisturbed soil | −0.807 | 22 | <0.001 |
| scarified soil + exposed soil | −0.411 | 58 | <0.01 |
| all treatments combined | −0.502 | 82 | <0.001 |

Figure 9 shows the densities of seedlings of all life-forms that were at least 10 cm in height after one year within the three soil surface treatments in relation to gap size. Clearly, larger gaps contain more tall seedlings, and the benefits of earlier germination in disturbed soil lead to a greater number of seedlings in the taller classes.

The height of the tallest individual tree in each gap shows a clear correlation with gap size even after 1 year (figure 10). After 3 years, the tallest tree was about 8 m, in the largest gap. Only a small part of these differences in maximum height may be attributed to larger sample sizes in the larger gaps. The erratic pattern of height amongst the smaller gaps is mainly due to the death of some of the leading plants and their replacement by different individuals. The fastest growth was mostly amongst tree species, notably *Cratoxylum sumatranum* (Jack.) Bl. Maximum height growth amongst species (almost all specimens were in the largest gap, 4) varied between less than 1 m $y^{-1}$ and 3 m $y^{-1}$.

Height growth of *Cratoxylum* in gap 4 provides a useful test between competition treatments and among soil surface treatments (figure 11). The tallest trees of

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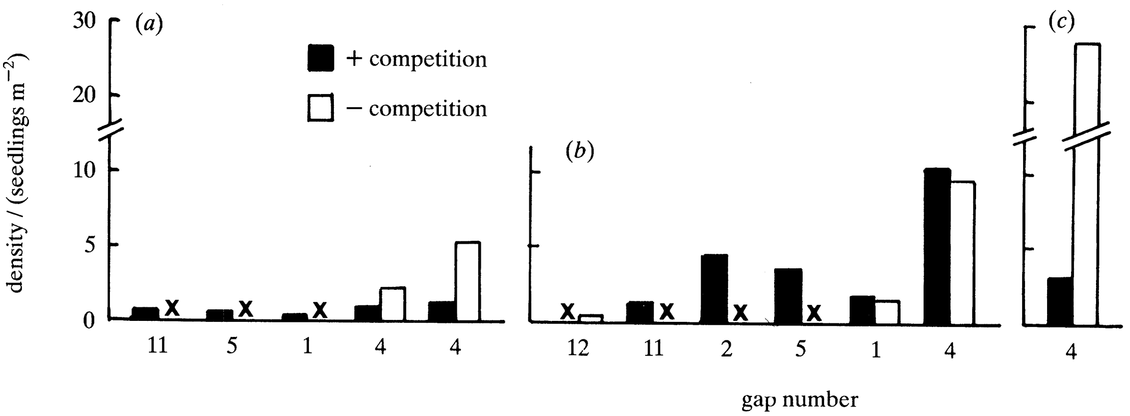

Figure 9. Density of seedlings at least 10 cm tall in each gap plot approximately one year after gap creation. Gaps arranged in order of increasing size. (*a*) Undisturbed-soil, (*b*) scarified-soil, and (*c*) exposed-soil treatments. The second pair of columns for gap 4 in (*a*) represents supplementary plots. X = treatment not applied.

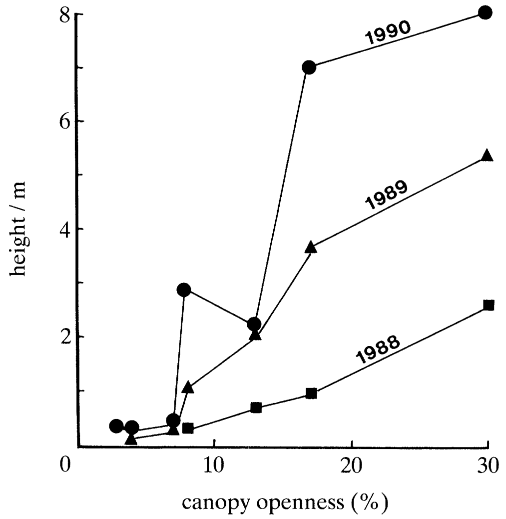

Figure 10. Height of single tallest colonizing tree plotted against canopy openness for one (1988), two (1989) and three (1990) years after the start of the study.

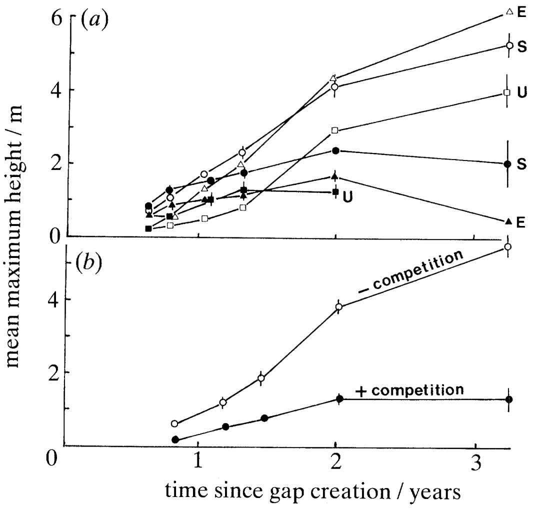

Figure 11. Changes over time in mean maximum height of *Cratoxylum sumatranum* seedlings in gap 4. (*a*) Experimental germination plots: each point is the mean of the five tallest individuals except for the final point of the lower 'E', a single plant. Solid symbols, with competition; open, without. Circles (S), scarified soil; triangles (E), exposed soil; squares (U), undisturbed. All *Cratoxylum* in the undisturbed plot with competition were dead at three years. (*b*) Supplementary plots (undisturbed soil): means of 10 tallest individuals. In both (*a*) and (*b*), bars indicating ± 1 s.e. are shown where they exceed the size of the symbol.

*Cratoxylum* in the supplementary plots grew about four times as fast without competition (figure 11*b*). Growth of seedlings was initially faster from disturbed soil than from undisturbed soil, and after three years, the tallest five trees on disturbed soil were 1–2 m taller on average than those on undisturbed soil (figure 11*a*). In the treatments with competition, growth after the second year appears to have been retarded.

### (*e*) *Development of forest structure in gaps*

Considerable resprouting of stumps cut during felling was recorded in each of the three gaps sampled three months after gap creation. Overall, 84.6% of stumps produced one or more shoots (average 4.6 per stump), but there was no significant difference between the gaps sampled in the frequency of sprouting stumps ($\chi^2 = 10.7$, d.f. = 2, $p > 0.5$), in the number of shoots per stump ($\chi^2 = 17.5$, d.f. = 14, $p > 0.1$), nor in the length of the longest shoot ($\chi^2 = 14.3$, d.f. = 10, $p > 0.1$). There were, however, significant positive correlations between the number of shoots per stump and the length of the tallest shoot in each of the gaps ($r_s = 0.379$, 0.619, 0.474; d.f. = 49, 79, 106; all $p < 0.01$), suggesting differences among individual plants in resprouting ability.

The potential for forest redevelopment from stumps is thus unrelated to gap size, but it became clear that the subsequent growth of pre-existing plants varied considerably among gaps. The plot with competition in the largest gap (4) eventually developed a tall, very dense stand composed mainly of a mixture of pre-gap seedlings and stump resprouts. In July 1990, 3.25 years after gap creation, the top of this regrowth canopy was shared with surviving plants that had germinated after gap creation and was about 6–7 m high. In smaller gaps, the density and height of pre-existing and resprouting plants were generally less. Thus the potential effect of competition from other vegetation on colonizing seedlings was greater in large gaps (see above).

## 4. DISCUSSION

### (*a*) *Effect of soil surface treatment*

Disturbance of the soil surface, either by removal of surface litter or especially by shallow scarification, leads to more rapid and more abundant germination of seeds from forest soil. This is true for both gap conditions and closed forest (figure 2). The effect is probably caused by the greater number of seeds which become exposed to the changes in microclimate which can break dormancy. These results confirm those of Putz (1983) and Uhl *et al.* (1988), who found higher densities of pioneer seedlings on the disturbed soil of root-pits than on undisturbed soil in natural treefall gaps, although the difference in the latter study was not significant.

Large seedlings grow faster than small seedlings, so plants which germinate rapidly in disturbed soil have an early advantage which is manifested by faster height growth (figure 9). This early advantage persists so that after two years leading trees of *Cratoxylum* (for example) from disturbed soil are 1–2 m taller than those from undisturbed soil (figure 11).

At least in large gaps, the more rapid development and higher seedling density on disturbed soil means that competition between plants begins sooner, resulting in higher mortality rates (figure 7); an effect enhanced by competition with other regrowth in the unweeded plots.

### (*b*) *Effect of competition with pre-existing plants*

Competition with resprouting stumps and other plants surviving gap formation is most pronounced in larger gaps, but does not become marked until the second year. It causes suppression of smaller plants leading, initially, to higher numbers in the small height classes than in samples where competing vegetation was cut back (Kennedy 1991). Leading trees are significantly taller without this competition, most clearly so after 2 years. These effects are paralleled by the higher seedling mortality rates in the treatment with competition (figure 7) and are especially marked in seedling cohorts which germinated some months after gap creation, when the resprout regrowth was well developed. Similar effects probably contributed to the results of Uhl *et al.* (1988), which indicated that, four years after the creation of a multiple treefall gap, pioneer seedling density was higher where advance regeneration had been removed than where it was retained.

Competing regrowth appears to have relatively little effect on the rate of accession of species, or on the final number germinating. Indeed, in gap 4, where the regrowth was densest, diversity (H′) two years after gap creation appears to be somewhat elevated in the samples where competition was not removed (figure 5). Similarly, Brandani *et al.* (1988), studying natural gaps, found greater diversity of colonizers in the areas around the boles of the fallen trees, where the pre-existing seedlings and saplings were least disturbed, than in the root-throw zones, where little advance regeneration survived.

The overall effect of competition on new seedlings is negative, however, although only clearly so in the largest gap, and there is no evidence that seedlings are ‘nursed’ during establishment.

### (*c*) *Effects of gap size*

The potential effects of gap size on the processes of revegetation are diverse. There is no apparent influence on the resprouting of cut stumps, nor on the rate of accession of germinating taxa. No relationship was evident between gap size and the number of seeds germinating: only in closed forest was germination markedly poor. Thus it would appear that if a critical gap size exists for the germination of colonizing species, it is very small, with canopy openness of the order of 5%, which is within the range reported for undisturbed closed-canopy forest (Brown 1990).

Gap size, however, has a clear influence on the performance of established colonists. In general, height growth increases with increasing gap size (figure 10), while mortality rates decline (figure 8); both trends presumably reflecting the greater availability of photosynthetically active radiation in larger gaps.

These results imply that at Danum, above a very small minimum size, gaps exert little selective influence on the establishment of colonizers, in contradiction of much previous work. Pioneer plants, which form most of the germinating species in our data, are thought to germinate and establish only if the soil is exposed to direct solar radiation (Swaine & Whitmore 1988). Our data enable this definition to be refined. It was found that some pioneer trees can germinate in very small openings, although not in large numbers (e.g. *Macaranga hypoleuca*, *Endospermum peltatum*; Appendix). These results support those of Raich & Gong (1990), which indicate that, although the seeds of pioneer species germinate best in large gaps, low levels of germination can occur even in closed forest. The apparent absence of pioneer seedlings from closed forest is thus probably more the result of poor growth and early mortality than of failure to germinate. Very young seedlings of pioneers in closed forest are easily overlooked because of their small size and ephemeral nature. The definition of pioneers offered by Swaine & Whitmore (1988) was too crude and needs more precise formulation.

Brokaw (1987) proposed that different pioneer species in the Costa Rican forests he studied have different minimum gap sizes for establishment, but his data (figure 1, p. 13) can equally well be explained as a sampling artifact. The chance of a tree growing in a gap is related to gap area and the abundance of the species in the forest. Thus, uncommon species are much less likely to appear in small gaps than in large. In Brokaw's data, there is a clear relationship between total species abundance and the size of the smallest gap in which it occurs. Thus *Trema micrantha*, with only 16 trees, first appears in a gap of 400 $m^2$, whereas *Miconia argentea*, with 66 trees, appears first in a gap of only 100 $m^2$. Brokaw's (1987, figure 1) observed minimum gap size for each species shows a close correlation with the total gap area/number of trees quotient. Some support for Brokaw's view, however, is provided by Raich & Gong (1990), who reported better germination of some pioneer species in a relatively small gap than in a large clearing.

The composition of the regrowth in our data shows no clear relationship with gap size (ordination, Kennedy 1991) and our species have distributions among the gaps too restricted to reveal differences in their mortality rates in gaps of different size (the necessary test of Brokaw's hypothesis). Although early mortality declines with increasing gap size, we have no evidence, for the moment, that this is a selective process affecting some species more than others. This matter can only truly be resolved by detailed investigation of the responses of the seeds and seedlings of individual pioneer species under controlled experimental conditions.

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## APPENDIX

*Cumulative total number of seedlings for taxa germinating in artificial gaps of different size at the Danum Valley Conservation Area*

(Numbers are the total numbers of seedlings for all plots within gaps, irrespective of area. Nomenclature follows Kennedy (1991). CF, closed forest site.)

| species | gap number:<br>sample area / m²: | CF<br>18 | 12<br>10 | 11<br>20 | 2<br>8 | 5<br>16 | 1<br>32 | 4<br>60 |
|---|---|---|---|---|---|---|---|---|
| Trees | | | | | | | | |
| Annonaceae sp.1 | | | 1 | | 2 | | | |
| *Carallia* cf. *borneensis* | | | 1 | 1 | | | | 1 |
| *Cratoxylum* cf. *sumatranum* | | | | | | 1 | | 625 |
| *Diospyros* sp. | | | | | 13 | | | |
| *Endospermum peltatum* | | | | 4 | | | | 1 |
| *Eugenia* sp. | | | 1 | | | | | 2 |
| *Euodia glabra* | | 1 | 50 | 68 | 2 | 12 | 2 | 33 |
| *Ficus lepicarpa* | | | | | 1 | | | |
| *Ficus* sp. E | | | | | | | | 1 |
| *Fordia* sp. | | 1 | | | | 5 | | |
| *Glochidion* cf. *elmeri* | | 1 | 5 | 4 | 6 | 3 | 15 | 27 |
| *Glochidion lutescens* | | | 1 | 4 | 7 | | 8 | 9 |
| *Glochidion rubrum* | | | 2 | 4 | 2 | | 13 | 3 |
| *Lithocarpus* sp. | | | | | | | | 1 |
| *Macaranga conifera* | | 2 | 1 | 4 | | | 3 | 4 |
| *Macaranga hypoleuca* | | | 1 | | 1 | 1 | | 4 |
| *Maschalocorymbus* sp. | | | | 4 | 6 | 8 | 13 | 5 |
| cf. *Neonauclea* sp.A | | | | | | 1 | | |
| *Nephelium* sp. | | 1 | | | | | | |
| *Pleiocarpidia sandakanica* | | | 1 | | | | 1 | 1 |
| *Pternandra azurea* | | | | | | 3 | | 9 |
| *Terminalia* sp. | | | | | 1 | | 2 | 2 |
| unknown sp. V | | | | 2 | | | | |
| unknown sp. VI | | | | | | | | 1 |
| *Vitex pinnata* | | | | | | | | 8 |
| Erect shrubs and treelets | | | | | | | | |
| *Callicarpa involucrata* | | | | | 1 | 1 | | 1 |
| *Callicarpa longifolia* | | | | | | | | 1 |
| cf. *Ixora* sp. | | | 1 | | | 1 | | 1 |
| *Lasianthus* sp. | | | | 4 | | | | |
| *Leea* sp. | | | | | | 2 | | |
| *Maesa ramentacea* | | | | | 1 | | 1 | 5 |
| *Mallotus miquelianus* | | | | | | | 3 | |
| *Melastoma* cf. *normale* | | | 1 | 2 | 4 | 4 | 18 | 14 |
| cf. *Mitrella kentii* | | 1 | 3 | | | 2 | 1 | 3 |
| *Saurauia agamae* | | | | | | 1 | | |
| *Saurauia longistyla* | | | | | 3 | | 2 | |
| *Urophyllum glabrum* | | | | 2 | | 10 | 2 | 6 |
| Scandent and sprawling shrubs | | | | | | | | |
| *Ampelocissus* sp. | | | | | | | | 1 |
| Annonaceae sp. 2 | | | | | | 2 | | 4 |
| Apocynaceae sp. 2 | | | | | | | | 1 |
| *Aristolochia* sp. | | 1 | 1 | 5 | | 1 | | |
| *Breynia rhamnoides* | | | | | | | 7 | |
| *Coptosapelta tomentosa* | | | | | | | | 1 |
| *Diplectria divaricata* | | | | | | 2 | 2 | 3 |
| *Diplectria glabra* | | | | | | 6 | 4 | 1 |
| *Diplectria viminalis* | | | | | | 2 | | |

Appendix (*cont.*)

| | gap number: | CF | 12 | 11 | 2 | 5 | 1 | 4 |
|---|---|---|---|---|---|---|---|---|
| species | sample area / m$^2$ | 18 | 10 | 20 | 8 | 16 | 32 | 60 |
| *Dissochaeta annulata* | | | | 3 | 5 | 40 | 17 | 58 |
| *Dissochaeta* cf. *beccariana* | | | | | 1 | 2 | | 4 |
| *Dissochaeta gracilis* | | | | 2 | | 15 | 2 | 10 |
| *Dissochaeta rostrata* | | | | | 1 | 37 | | |
| *Dissochaeta* sp. B | | | | | | | | 1 |
| *Embelia ribes* | | | 1 | 5 | 2 | 3 | 1 | 1 |
| cf. *Fissistigma* sp. | | | | | 2 | | | |
| *Jacquemontia tomentella* | | | | 2 | 1 | | | |
| *Leguminosae* sp. 1 | | | | | | | | 1 |
| *Macrolenes* cf. *bipulvinatus* | | | | | 4 | 5 | 1 | 1 |
| *Macrolenes* sp. A | | | | | | 4 | 1 | 4 |
| *Macrolenes* sp. B | | | | | | 1 | | |
| *Merremia* sp. A | | | | | 4 | 1 | 2 | 3 |
| *Mussaenda* cf. *glabra* | | | 2 | 28 | | 11 | 14 | 25 |
| *Piper* sp. | | | | | | | 1 | |
| *Smilax* sp. | | | | | 1 | | | |
| *Tetrastimga* sp. | | | | 1 | 3 | | | |
| *Uncaria* sp. A | | | 3 | 1 | 12 | 4 | 4 | 7 |
| *Uncaria* sp. B | | | 1 | | | 1 | | 1 |
| *Uncaria* sp. C | | | | | 3 | 2 | 2 | 13 |
| *Uncaria* sp. G | | | 2 | 4 | 1 | 19 | 15 | 118 |
| *Uncaria* sp. H | | | | | | 1 | 2 | 2 |
| *Uncaria* sp. J | | | | | | 1 | | 1 |
| Vitaceae sp. 1 | | | | 1 | | | | |
| Bole climbers | | | | | | | | |
| *Ficus* cf. *aurantiacea* | | | | 3 | 2 | | | |
| *Ficus punctata* | | 1 | | 1 | | 1 | 2 | 7 |
| Rubiaceae sp. 1 | | | 1 | | | 1 | 22 | 2 |
| unknown sp. I | | | | 2 | | | 1 | 6 |
| Herbs | | | | | | | | |
| *Begonia* sp. | | | | | 3 | | | |
| *Blumea balsamifera* | | | | | | | 2 | 2 |
| *Borreria meyeniana* | | | | 5 | 3 | 17 | 25 | 6 |
| Compositae sp. 1 | | | 1 | 3 | | 3 | | |
| Compositae sp. 2 | | | | | | | 1 | 2 |
| *Costus* sp. | | | 1 | 1 | | | | |
| Cucurbitaceae sp. | | | 1 | 1 | | | 1 | |
| cf. *Cyperus* sp. | | | | | | | | 8 |
| *Cyrtandra* sp. | | | | | 15 | 1 | | |
| *Eupatorium odoratum* | | | | | | | | 2 |
| *Imperata cylindrica* | | | | | | | 1 | 1 |
| *Mapania* sp. | | | | | | 89 | | |
| *Ophiorrhiza* sp. | | | | | 28 | | 7 | |
| *Paspalum conjugatum* | | | | | | | 50 | 1 |
| Rubiaceae sp. 2 | | | | | 1 | | | |
| Rubiaceae sp. 3 | | 404 | 2 | 1 | | | | |
| *Xanthophytum fruticulosum* | | | | | 40 | | | |
| Zingiberaceae spp. | | | 1 | 5 | 3 | 5 | | 3 |
| unidentified | | 141 | 13 | 48 | 35 | 61 | 83 | 58 |
| total | | 554 | 99 | 222 | 218 | 393 | 354 | 1127 |
| number seedlings per square metre | | 30.8 | 9.9 | 11.1 | 27.2 | 24.6 | 11.1 | 18.8 |