CHAPTER 5

LIMITING STAGES

5.1 Introduction

To develop methods of accelerated natural regeneration (ANR) for cleared areas of forest, it is necessary to know which species fail to colonize clearings naturally and what factors prevent them from doing so. A systematic approach to this problem is to study the colonization process by stage and to compare the performance of different species at each stage.

At the species level, each life-cycle stage can be considered as a filter through which some or all individual seeds or seedlings may fail to pass (Keddy, 1992). A *critical stage* is defined here as a stage where all individuals fail to pass through the filter and colonization by that species is blocked, or undetectable at the level of sampling used in this study. The species is thus *excluded* from colonizing the clearing (*sensu* Grubb, 1987). An *inhibiting* stage is defined as a stage where many individuals of a species fail to pass through the filter, reducing the probability of colonization in comparison to more successful species. A *limiting stage* is used in a general sense to represent a stage which may lower the probability of colonization, when the extent of this effect is not known, not relevant or varies between species.

Many studies have shown that critical and inhibiting stages vary between species and that this can be linked to certain morphological species traits.

The dispersal stage. — Large seeded-species are particularly likely to be filtered out of the colonization process at the dispersal stage. "Heavy-seeded, animal-dispersed" species were conspicuously underrepresented in rights-of-way in New York, USA and this was attributed to very low rates of dispersal (Hill *et al.*, 1995). One mechanism for the filtration of large seeds is the consumption capacity of seed dispersing vertebrates. In abandoned Amazonian pasture, no seeds larger than 16 mg were found in the faeces of birds and bats (Nepstad *et al.*, 1996), while in another study in the same region, seeds in bird faeces were mostly of small-seeded shrub and pioneer tree species and did not exceed 13 mm in length (da Silva *et al.*, 1996).

The recruitment stage. — There is some evidence that very small seeded species fail at the recruitment stage in mid-successional clearings. *Betula* and *Populus* species were poorly represented in vegetated rights-of-way (Hill *et al.*, 1995) and no seedlings of *Betula pendula* were found in a 35 year old chalk quarry in England despite the presence of older saplings (Finegan, 1984).

The establishment stage. — Mortality of 1st-year seedlings can be an important filter on relative establishment success of tree species in old clearings (e.g. De Steven, 1991). In seasonal tropical climates, species which have the ability to die back during the dry season then resprout in the rainy season have a clear survival advantage (Gerhardt, 1994). Nepstad *et al.* (1990) highlighted the importance of drought tolerance in enabling species to pass through the 1st-year establishment filter and predicted that large-seeded species were more likely to show this trait.

Several studies have compared the relative importance of different life-history stages in determining the species composition of the seedling community. McClanahan and Wolfe (1993) monitored the seed rain on a Florida mine-site and calculated seedling recruitment indirectly by comparing the seedling density accumulated over seven years with the seed rain observed over 20 months. However, they made no distinction between recruitment from resprouting of rootstocks and germination from seed. In this physically harsh environment, recruitment was a stronger filter than dispersal for large-seeded, late successional species, as many failed to establish despite being present in the seed rain. Dalling *et al.*, (1998) compared dispersal limitation with establishment limitation in treefall gaps on Barro Colorado Island, Panama and found that both were important determinants of local abundance. Seed dispersal was inferred by analysing the distance between seedlings and the nearest conspecific reproductive adult. In rights-of-way in New York, Hill *et al.* (1995) found that the relative importance of dispersal and establishment as the inhibiting stage was best predicted by seed size and dispersal mode.

This chapter focuses on the early stages of tree colonization of abandoned agricultural clearings and will define and compare the filtering effect of seed dispersal, seedling recruitment and seedling survival to the end of the first dry season. The study of dispersal was limited to air-borne seed dispersal by birds, bats and wind as opposed to ground-based secondary dispersal by animals. Recruitment is defined here as the emergence of seedlings of at least 5 cm in height, thus amalgamating the two distinct stages of germination and germinant survival to 5 cm for practical reasons. Although the seedling cannot be considered to have successfully colonized the clearing until if forms part of the dominant vegetation canopy, the later stages of survival and growth were beyond the scope of this thesis.

If seed dispersal is a limiting factor, then the seed rain would be expected to be more abundant at the clearing edge than at the centre. The edge zone presents an opportunity to study clearing recruitment and establishment of poorly dispersed species which may not be present in the clearing centre due to their absence from the seed rain.

Specific questions are:

- For each species, what is the critical and inhibiting stages in the colonization of abandoned agricultural clearings?

- Are there species traits which predict which stage is critical or inhibiting?
- Is tree colonization less in clearing centres than in clearing edges?

5.2 Methods

5.2.1 Species identification and characteristics

This study included all species encountered in the field observations which could be identified as tree species. Species were identified by comparing seed and seedling samples with identified plants growing at each site, or with herbarium specimens held at Chiang Mai University (CMU), the Natural History Museum, London and the Forest Restoration Research Unit (FORRU), Doi Suthep-Pui National Park, ensuring that very few, if any, tree species were excluded.

Lifeforms were primarily assigned to species using the CMU database, recording both "trees" and "treelets" as "trees" for this study. A few "treelets" were reclassified here as "shrubs", base on my own observations or descriptions in the floras and on herbarium specimens at the Natural History Museum, London (Appendix I).

Seed lengths were taken from Pakkad, (1997), if available or were measured directly from seeds collected in the traps or from seed specimens at FORRU. A "seed" was defined as the anatomical seed plus any attached non-dehiscent hard fruit tissue, but excluding external fleshy or dehiscent fruit tissue or wings. For example, *Eleaocarpus* "seeds" include the hard stony endocarp which is anatomically fruit tissue.

Data sources on seed dispersal and germination times included this study, Hardwick and Elliott (1992), the FORRU database (unpublished) and personal observations in the field (see Appendix I for germination syndromes).

5.2.2 Field data

5.2.2.1 Seed dispersal

The seed rain was monitored monthly for 2 years (June 1994 - May 1996) at 3 replicate sites (Chapter 2). At each site, six seed traps were placed in each of three zones, clearing centre, clearing edge and forest, giving a total of 54 traps overall. The clearing centre was defined as the area at least 10 m away from the forest edge. It was divided into six equal sized sub-sections and one trap was randomly placed in each. The clearing edge zone was the peripheral area of the clearing, 10 m in width, adjacent to the forest and it was subdivided into north and south facing edges. Three traps were placed along each edge, one randomly located within each of three equal-sized sub-sections. The forest zone was the area between 10 and 100 m distance from the clearing: traps were placed at least 20 m apart as suggested by Terborgh (1983) in areas with continuous canopy.

Each circular seed trap was 1 m^2. Plastic mosquito netting with a 1.7mm mesh was stitched onto a wire frame which was supported about 50 cm above the ground on bamboo legs and adjusted to be horizontal. In the field, vegetation directly above the traps was undisturbed.

Traps were emptied monthly by picking large leaves out of the trap, then sweeping the remaining contents into plastic bags, along with material caught on a sheet placed below the trap while it was emptied. If wet, the contents of the traps were air-dried in trays in the lab.

Contents of the traps were sorted through by hand in the lab. Seeds were identified to species or named unknown morphotype and a dried sample of each was kept. All seeds of forest tree species or unidentified morphotypes were counted. Where seed predation had occurred the original number of seeds was estimated from fruit and seed remnants. Clearly immature seeds were not counted.

5.2.2.2 Germination and seedling establishment

Seedling recruitment was monitored in 54 permanent sample plots, each 4 m by 1 m and placed 2 m from each seed trap in the three sites. Four seedling censuses were carried out: November 1994 (t0: end of rainy season), May 1995 (t1: end of dry season), December 1995 (t4: end of rainy season) and May 1996 (t5: end of dry season). All tree seedlings over 5 cm tall were individually marked with an aluminium tag secured to the ground with a wire pin. Data from each square metre of the plot were recorded separately to permit the calculation of the mean density of species per m^2. Seedling recruitment was measured for the thirteen month period t0 to t4 (November 1994 to December 1995). Survival and growth of new recruits, marked at t2 and t4 was measured between t1 and t5 (May 1995 to May 1996) . (Fig. 5.0 – all tables at end of chapter). Thus t1 recruits were followed for 12 months, but t4 recruits were only followed for five months.

5.2.3 Analysis

5.2.3.1 Determination of community level filtration process

To compare community level filtration between sites and habitats, species density (the number of species per unit area) was used rather than total number of species per plot, to enable direct comparison between the seed and seedling stages despite different sampling areas. Sp. density better indicator of success than seed de[nsity] as seeds always dominated by a single tiny seeded

Species density was calculated at four colonization stages: seed rain in the forest (ie seed source), seed rain in the clearing (ie dispersed seed), the cumulative number of recruits during the 1995 growing season (measured at t1 and t4) and the survival of recruits by the end of the 1995-96 dry season (measured at t5).

Three filters were calculated as the percentage decline in species density between stages:

- Dispersal filter: species density of seed rain in the clearing divided by that of seed rain in the forest, multiplied by 100.
- Recruitment filter: species density of new recruits in t1 and t5 divided by speices density of sed rain in the clearing, multiplied by 100.
- Survival filter: species density of surviving recruits at t5 dividied by species density of new recruits in t1 and t4, multiplied by 100.

Table 5.1. The stages of colonization observed in this study and the life-cycle filters which link them

Observed stage	Life-cycle filter
Forest seed rain	
	Seed dispersal
Clearing seed rain	
	Seedling recruitment
Clearing recruits	
	Seedling survival
Clearing survivors	

Filters were calculated separately for the centre and edge zones of the clearing at each site.

There was no significant difference in annual species density of seed rain between year 1 and year 2 (3- way ANOVA with year, site and zone as factors, df = 1,90, F = 0.86) (Fig. 5.1). Therefore, mean density per plot for years 1 and 2 was used.

A two-way ANOVA, with site and colonization stage as factors, was performed on log transformed species density. This was done separately for the clearing edge and clearing centre zones. Individual comparisons were made using Tukey's pairwise comparison with a family error rate of 0.05.

5.2.3.2 Determination of filtration process by species

At each site, all tree species recorded at one or more of the stages of colonization of the clearing centre were listed. Species present at low densities may have been missed in later stages due to sampling errors. Species found in later stages, but absent in earlier stages were assumed to have been missed in earlier stages due to sampling error or, for the dispersal stage, to have undergone "ground-borne" dispersal, which was not detected by the seed traps. Each species was scored for frequency at each site as the number of traps or plots out of six in which it was recorded and the species in each site list were divided into "filter groups" according to the last stage at which each species was observed. The number of species progressing through to recruitment and survival was so small that these two stages were combined.

Table 5.2 Definition of filter groups used to classify tree species at each site.

Group	Ultimate stage where species observed	Phase in which species filtered out
D	Seed rain in forest	Dispersal
R	Seed rain in clearing	Recruitment
E	Recruits and survivors in clearing	Established seedlings present at end of first dry season

When considering the filtration of individuals of a particular species, it was important to follow the same cohort of seeds from dispersal through recruitment and survival, because of between year variation in seed production of individual species. As there is often a long delay between seed dispersal and seed germination in seasonal tropical forests, especially for species dispersed late in the rainy season or dry season (Garwood, 1983), one 12-month period of seed rain data is not appropriate for all species whose seedlings recruited in t1 and t4. To select the appropriate 12-month period from the 24 month seed rain data, each tree species in this study was assigned to one of five groups (modified from Garwood, 1983), based on the timing of seed germination relative to seed dispersal (see 5.2.1 for source of data).

1. **Early rapid rainy group:** seeds are dispersed early in the rainy season and germinate in the same rainy season.
2. **Late rapid rainy group:** seeds are dispersed late in the rainy season and germinate from the end of the same rainy season through to the beginning of the immediately following cold, dry season.
3. **Delayed rainy group:** seeds are dispersed in the rainy season but do not germinate until the following rainy season.
4. **Intermediate dry group:** seeds are dispersed in the dry season and germinate in the following rainy season.
5. **Continuous group:** seeds are dispersed continuously throughout the year, or sporadically with no regular pattern (germination time unknown).

The relevant 12-month period of seed rain for species in the delayed rainy and the late rapid rainy groups was from June 1994 to May 1995. The relevant 12-month period for the intermediate dry, early rapid rainy and continuous groups was November 1994 to October 1995.

5.2.3.3 Analysis of filtration process in relation to seed size

Dispersal and recruitment success were measured for each species, separately for each site and zone. The "dispersal success ratio" (DSR) for each species was calculated as the density of clearing seed rain divided by the density of the forest seed rain. The "recruitment success ratio" (RSR) for each species was calculated as the density of clearing seed rain divided by the density of the forest seed rain. Survival success was measured directly by monitoring the survival of each seedling from recruitment to the end of the first dry season, pooling over all sites and zones because of low sample sizes. The survival success ratio (SSR) was the total number of survivors divided by the total number of recruits. All densities were calculated for the single cohort of seeds and seedlings as described above.

Each success ratio was plotted against seed size and compared through regression or visual analysis.

5.3 Results

5.3.1 Community level filtration process

5.3.1.1 Species density at each stage

Species density declined from stage to stage in both clearing centres and edges (Fig. 5.2). Species density in the forest seed rain was 11-14 species m^{-2} and declined to < 1 species m^{-2} at the recruit stage, in both zones of the clearing. The species density of survivors after the first dry season was slightly lower than that of recruits, but not zero (0.1-0.4 species m^{-2}). At least 94% of the original species density was lost during dispersal and recruitment and only 0 to 3% was lost during establishment. There was very little difference between forest and clearing in the species density of recruits and survivors.

The relative fall in species density between stages is of greater interest for understanding the mechanics of the filtration process. The greatest relative reduction was during recruitment (Fig. 5.3), averaging 92 to 95%. Filtration was more variable between sites and zones during dispersal and survival than during recruitment (Fig. 5.3).

5.3.1.2 Inter- site differences in species density

Forest seed rain

There was no significant difference in species density between sites despite differences in tree density described in Chapter 2. Mean species density in the forest seed rain was 12.8 species.m^{-2} yr^{-2}, averaged over all sites.

Colonization of clearing edge: seed rain, recruits and survivors

There was a highly significant difference in species density between stages (df = 3, F = 237.5, $P < 0.001$) and a significant interaction between stage and site (df = 6, F = 2.35, $P < 0.05$), although site had no overall effect. The interactive effect was evident at the seed rain stage: Site 3 had a significantly lower species density than Site 2 (5.7 ± 1.5 species m^{-2} compared with 11.6 ± 1.6.

Colonization of clearing centre: seed rain, recruits and survivors.

The patterns observed at the clearing centre were more marked in the clearing edge (Fig. 5.2). There was a significant difference in species density between sites (df = 2, F = 10.3, $P < 0.001$) and between stages (df = 3, F = 285.9, $P < 0.001$) and a significant interaction between the two (df = 6, F = 3.2, $P < 0.05$). A further F-test on the site vs. interaction mean square, showed that the site effect was largely due to the interaction seen at the seed rain stage (F = 3.25, not significant). Species density at Site 3 was significantly lower than both the other sites at the seed rain stage (2.7 ± 0.5 species m^{-2} compared with 7 ± 0.6 at Site 1 and 8.6 ± 0.9 at Site 2. Relative filtration at Site 3 was 79%, compared with only 38% and 34% at Sites 1 and 2, respectively (Fig. 5.3). Species density of recruits and survivors at Site 3 was also slightly lower than at the other two sites (0.1 compared with 0.3 species m^{-2}) but not significantly so. Pairwise comparisons showed no significant difference between Sites 1 and 2 at any stage.

5.3.2 Filter groups

5.3.2.1 Inter-site differences in critical stage

Distribution of species into the three filter groups is shown in Table 5.3 for each site. From a pool of 53 species recorded in at least one stage in the forest or clearing centre, only eight species had successfully established in the clearing centre of at least one site by the end of the dry season. Less than 20% of potential colonizing species at any site established seedlings. All other species were filtered out either during dispersal or recruitment. Although the number of species filtered out at dispersal and recruitment varied between sites (groups D and R), the size of both groups was always greater than the number of species establishing (group E) at each site.

Species behaviour varied among sites. Thirty one species (58%) occurred at more than one site; of these, 17 (55% - about one third of the total species pool) were filtered out at different stages at different sites. *Morus macroura*, for example, was filtered out during recruitment at Site 1 but during dispersal at Site 3.

5.3.2.2 Seed size in relation to filter groups

The relationship between filter groups and seed size was examined to determine the net effect of seed size on dispersal and establishment. The species which successfully dispersed (those in groups R and E) were significantly smaller than those which failed to disperse (those in group D), (2-way ANOVA on effect of site and group on log transformed seed size, df = 1,88, F = 14.9, $P < 0.001$). Of the species which did disperse, those that successfully established (group E) were significantly larger than those which failed to establish (group R), (2-way ANOVA as above, df = 1,35, F = 12.8, $P < 0.01$). The net effect of the above was that there was no significant difference in mean seed size between groups D and E, but species in both groups had significantly larger seeds than species in group R (Tukey's pairwise comparison with a family error rate of 0.05, see Fig.5.4).

These results confirmed the importance of seed size at each stage of the colonization process. Further analyses were carried out on the tracked cohort of seeds and seedlings to determine the parameters within which dispersal and establishment could progress successfully.

Table 5.3. Site species lists, with species grouped according to the stage at which they were filtered out of colonization of the clearing centre. Table also shows the number of traps or plots (out of a maximum of six) in which each species was represented at each of the four stages.

SITE 1

Group	Species	FSR	CSR	Rec	Surv
D	*Turpinia nepalensis*	4			
	Beilschmiedia sp. 1	2			
	Manglietia garrettii	2			
	Symplocos macrophylla	2			
	Antidesma bunius	1			
	Castanopsis diversifolia	1			
	Castanopsis tribuloides	1			
	Cinnamomum caudatum	1			
	Ficus semicordata	1			
	Vitex quinata	1			
R	*Betula alnoides*	6	6		
	Debregeasia longifolia	6	6		
	Schima wallichii	6	5		
	Trema orientalis	4	4		
	Eurya acumminata	5	4		
	Macropanax sp. 1	1	2		
	Litsea cubeba	3	2		
	Glochidion acuminatum	4	2		
	Saurauia roxburghii	5	2		
	Aporusa villosa		1		
	Erythrina stricta		1		
	Anneslea fragrans	1	1		
	Morus macroura	3	1		
	Vernonia volkameriifolia	6	1		
E	*Engelhardia spicata*	6	6	3	2
	Helicia nilagirica			1	1
	Prunus cerasoides	4	2	1	1

SITE 2

Group	Species	FSR	CSR	Rec	Surv
D	*Antidesma bunius*	5			
	Acronychia pedunculata	4			
	Castanopsis tribuloides	3			
	Manglietia garrettii	3			
	Rhus chinensis	3			
	Elaeocarpus prunifolius	2			
	Castanopsis acuminatissima	1			
	Eugenia albiflora	1			
	Fraxinus floribunda	1			
	Helicia nilagirica	1			
	Lithocarpus elegans	1			
	Macaranga kurzii	1			
	Rhus succedanea	1			
	Styrax benzoides	1			
	Turpinia pomifera	1			
	Vitex quinata	1			
R	*Betula alnoides*	6	6		
	Ficus superba	6	6		
	Adinandra integerrima	5	6		
	Trema orientalis	5	6		
	Debregeasia longifolia	4	3		
	Vernonia volkameriifolia	4	3		
	Mallotus paniculatus	2	3		
	Eurya acumminata	6	2		
	Symplocos macrophylla	6	2		
	Glochidion sp. 1		1		
E	*Macaranga denticulata*	4	2	2	
	Eugenia claviflora	5	1	1	
	Schima wallichii	6	6	2	1
	Mischocarpus pentapetalus	1	3	2	1
	Prismatomeris tetrandra	1		1	1
	Actinodaphine henryi			1	1

SITE 3

Group	Species	FSR	CSR	Rec	Surv
D	*Symplocos macrophylla*	6			
	Vernonia volkameriifolia	6			
	Trema orientalis	5			
	Acronychia pedunculata	3			
	Castanopsis tribuloides	3			
	Cryptocarya sp. 1	3			
	Eugenia claviflora	3			
	Helicia nilagirica	3			
	Litsea salicifolia	3			
	Morus macroura	2			
	Saurauia roxburghii	2			
	Actinodaphine henryi	1			
	Alstonia glaucescens	1			
	Beilschmiedia sp. 1	1			
	Castanopsis acuminatissima	1			
	Debregeasia longifolia	1			
	Engelhardia spicata	1			
	Glochidion sp. 1	1			
	Lauraceae sp. 1	1			
	Macropanax sp. 1	1			
	Mallotus paniculatus	1			
	Phyllanthus roseus	1			
	Prismatomeris tetrandra	1			
	Rhus succedanea	1			
	Styrax benzoides	1			
	Vitex quinata	1			
	Xanthophyllum flavescens	1			
R	*Betula alnoides*	6	6		
	Fraxinus floribunda	1	2		
	Eurya acumminata	6	1		
	Rhus chinensis	3	1		
	Adinandra integerrima		1		
E	*Prunus cerasoides*	2		1	
	Macaranga denticulata	1		2	1
	Schima wallichii	6	2	1	1

[a] Groups as follows: D = filtered out at dispersal, R = filtered out at recruitment, E = successfully recruited (most had established by end of dry season).
[b] Stages as follows: FSR = forest seed rain, CSR = clearing centre seed rain; Rec = new seedling recruits in clearing centre, at least 5 cm high; Surv = recruits surviving first dry season.

5.3.3 Limiting stages in relation to seed traits

5.3.3.1 Dispersal phase

All results presented here on the dispersal phased refer to the cohort of seeds contributing to the recruitment of seedlings in the growing season of 1995.

Source of origin. — Seeds of tree species that were observed fruiting in the clearing at a particular site were considered to be of possible clearing origin and all other species were designated as being of forest origin, even if the species were not actually recorded in the forest. At all three sites more than 77% of the tree species in the clearing edge and centre seed rain originated in the forest. Further analysis concentrated on these species, although the species of possible clearing origin are shown in Fig. 5.5 for comparison.

Proportion of each dispersal modes. — The proportion of wind dispersed species in the seed rain was lowest in the forest zones(15-19%), increasing through the clearing edges (18-31%) to the clearing centres (25-60%). The high proportion of wind dispersed seeds in the clearing centre at Site 3 (60%) was due to a particularly low incidence of animal dispersed seeds (only two species compared with nine at each of the other two sites) rather than a high number of wind dispersed species, of which there were three (compared with four at Site 1 and three at Site 2).

Abundance vs. seed size. — A single measurement of abundance for each species in each habitat zone (forest, clearing edge and clearing centre) was calculated by adding together the totals from the three sites. The abundance in each zone was then compared with seed size (Fig. 5.5). In all three zones the maximum density of air-borne seeds declined sharply with increasing seed size (Fig. 5.5), but the seed density of a particular species was unpredictable, falling anywhere between zero and the maximum limit for its seed size. At a given seed size, wind dispersed seeds were generally more numerous than animal dispersed seeds by about an order of magnitude, although this again was highly variable.

Maximum size of air-borne seed in each zone. — The size of the largest seed collected in the forest was 29 mm long (*Beilschmiedia* sp. 1); in the clearing edge it was 20 mm long (*Markhamia stipulata* – air dispersed) and in the clearing centre, 12 mm, (*Eugenia claviflora*), (Fig. 5.5 and table below).

Table 5.4. Size of the largest seed collected in the seed rain in each zone in each site. The sample of seed rain is the cohort of seeds contributing to seedling recruitment in the rainy season of 1995.

Site	Forest		Clearing edge		Clearing centre	
	Species	Seed (mm)	Species	Seed (mm)	Species	Seed (mm)
1	*Beilschmiedia* sp.1	29	*Prunus cerasoides*	10	*Prunus cerasoides*	10
2	*Helicia nilagirica*	20	*Bridelia pubescens*	9	*Eugenia claviflora*	12
3	*Beilschmiedia* sp.1	29	*Markhamia stipulata*	20	*Fraxinus floribunda*	7

Relative dispersal success (as measured by the dispersal success ratio, see methods) was calculated for the species recorded in the forest seed rain at each site (Fig.5.6). Species which were recorded in the clearing but not in the adjacent forest seed rain were excluded from the analysis as they had a dispersal ratio of infinity (Table 5.5). These species were a minority in both the clearing edge (18 ± 5% of species and 0.6 ± 0.5% of seeds, mean and standard error of three sites) and clearing centre (15 ± 3% of species and 0.3 ± 0.1% of seeds). Most of these species were represented by only one or two seeds and were scarce as fruiting trees at the site in question.

Table 5.5. Species recorded in clearing seed rain which were absent from forest seed rain.

Clearing edge				Clearing centre			
Site	Species	Seed size	n	Site		Seed size	n
1	*Styrax benzoides*	4	1	1	*Aporusa villosa*	9	1
2	*Morus macroura*	1	11		*Erythrina stricta*	11	1
	Glochidion sp. 1	3	1	2	*Glochidion* sp. 1	3	4
	Albizia odoratissima	8	1	3	*Adinandra integerrima*	3	2
	Bridelia pubescens	9	1				
3	*Litsea cubeba*	6	2				
	Manglietia garrettii	6	1				
	Markhamia stipulata	20	9				
	Adinandra integerrima	3	11				

The dispersal success of species observed in the forest seed rain can be seen as falling into three groups: (1) those which were not recorded in the clearing at all (average and standard error for three sites is 50±7% in edge zones and 65±12% in centres), (2) those which were recorded in the clearing at a lower density than in the forest (35±12% in edges and 25±10% in centres) and (3) those which were found in the clearing at a higher density than in the forest (15±4% in edges and 10±4% in centres). The last and smallest group is of particular interest as these species apparently dispersed preferentially into the clearings. Extraordinarily high dispersal ratios were seen in some species at the clearing edge, where a single seed trap happened to fall adjacent to a fruiting tree: *Ficus superba* and *Mischocarpus pentapetalus* at Site 2 and *Macaranga denticulata* at Site 3, had ratios of 1951, 84 and 139 to one respectively. At Site 2 the ratios were still high in the centre zone (1.2 and 5) but at Site 3 the ratio had fallen to 0. Most of the species with a dispersal ratio greater than one to one could be linked to a large tree close to the clearing edge.

There was no discernible relationship between relative dispersal success and seed size

5.3.3.2 Recruitment phase

Most species in the seed rain failed to recruit: in the clearing edges only 16 ± 3% of dispersed tree species produced recruits and in the clearing centres only 20 ± 5% (percentage of tree species recorded as dispersing or recruiting, mean and standard error of 3 sites, Figs. 5.7 and 5.8). The burning of Site 3 in the dry season of 1995 did not reduce the overall percentage of dispersed species recruiting in either the clearing edge (13% compared to 13%, Site 1 and 23%, Site 2) or clearing centre (17% compared to 13%, Site 1 and 29%, Site 2). However, Site 3 did differ from the other two sites in that none of the animal dispersed species in the seed rain recruited, even though recruitment of wind dispersed species was the same as or higher than at Sites 1 and 2. Two animal dispersed species did recruit at Site 3 (*Spondias axillaris* in the edge zone, n = 4 and *Macaranga denticulata* in the centre, n = 3), but neither had been recorded in the seed rain in the zone where they recruited.

There were 55 new recruits (of 16 tree species) in the clearing edge zones and 33 new recruits (of nine tree species) the clearing centre. Almost all the new recruits germinated from seed originating in the forest, with only one species (*Macaranga denticulata* at Site 2) possibly originating from trees which had previously colonized the clearings.

Two wind dispersed species recruited into the clearing edges (*Schima wallichii* and *Markhamia stipulata*) and two into the clearing centres (*Schima wallichii* and *Engelhardia spicata*), making up 22% and 13% of all recruiting species respectively and 35% and 30% of all individuals. The average density of wind dispersed recruits was 0.26 seedlings m^{-2} at the clearing edge and 0.14 seedlings m^{-2} at the centre. Three wind dispersed species failed to recruit from the clearing seed rain. The two smallest-seeded species (*Betula alnoides*, 1mm and *Vernonia volkameriifolia*, 3 mm) both failed, despite dispersing large numbers of seed: a total of 3718 and 190 seeds were trapped across all sites and clearing zones combined (i.e. 36 traps). *Fraxinus floribunda*, with larger seeds of 7 mm, also failed to recruit, but the seed supply was much smaller: only four seeds were trapped in the clearings.

The recruitment ratio of medium sized wind dispersed seeds (*Schima wallichii* and *Engelhardia spicata*) was low in both areas of the clearing at Sites 1 and 2, ranging from 0 to 0.02. The ratio of *Schima wallichii* at Site 3 was much higher, 0.125, a result which may have been influenced by the fire at Site 3 immediately prior to dispersal of *Schima wallichii* seed. The only large seeded species, *Markhamia stipulata*, had a very high recruitment ratio of 0.42.

Animal dispersed species made up the greatest proportion of new recruits, with a total of 14 species recorded and an average density of 0.50 seedlings m^{-2} at the clearing edge and seven species and an average density of 0.32 seedlings m^{-2} in the centre.

In the clearing edges, new recruits were randomly distributed along a seed-size gradient stretching from 2 mm to 29 mm while in the clearing centres seed sizes ranged from 2 mm to 20 mm (Fig. 5.7). However, the effect of seed size on recruitment success could only be judged for species with seeds up to 12 cm, as above this limit no seeds were recorded in the clearing seed rain. Again, species with the smallest seeds failed to recruit in both the forest and clearing. *Debregeasia longifolia* (2214 seeds in the edge traps and 20,898 in the centre traps), *Saurauia roxburghii* (17 and 8), *Ficus superba* (1,262,310 and 776), *Eurya acumminata* (224 and 99) and *Morus macroura* (176 and 5) all had seeds under 2 mm long and all produced no new recruits.

Only 13 to 30% of species with medium sized seeds (2 to 12 mm) recruited new seedlings. In the successful species, the recruitment ratio was higher for animal dispersed than for wind dispersed species, ranging from 0.1 to 0.3 in the clearing centre. There was no significant correlation between seed size and recruitment ratio, (R^2 = 0.15 at Site 1 and 0.50 at Site 2).

In the edge zone half the recruiting animal dispersed species (64% of individuals) had not been recorded previously in the seed rain. These species had seeds of 10.4 to 29.2 mm, all of which were larger than those which *had* been observed in the seed rain. In the clearing centre zone three out of the seven species of animal recruits had not been observed in the seed rain. However, their contribution to the overall pool of recruits was small (only 13% of individuals) as each species was represented by just one seedling. One of the species, *Helicia nilagirica* (seed length, 20.4 mm) was larger than 12 mm, the upper limit of seeds in the clearing centre seed rain.

Where the seed density at the clearing edge was very high due to the close proximity of a parent tree, the recruitment ratio of individual species was decreased by at least an order of magnitude in comparison to the clearing centre (Table 5.6). In view of this complicating factor at the clearing edge, analysis of recruitment patterns was restricted to the clearing centre where density was not a factor. Analysis was further restricted to Sites 1 and 2, where recruitment was not affected by fire.

Table 5.6. Comparison of seed density and recruitment ratio at clearing edge and clearing centre.

Site	Species	Clearing edge		Clearing centre	
		Density	Rec.ratio	Density	Rec.ratio
1	*Prunus cerasoides*	9.5	0.004	0.8	0.25
2	*Macaranga denticulata*	15.5	0.008	1.8	0.11
2	*Mischocarpus pentapetalus*	14	0.009	0.8	0.3

In the clearing centres of Sites 1 and 2, the recruitment ratio of recruiting wind dispersed species was at least an order of magnitude less than that of recruiting animal dispersed species.

5.3.3.3 Establishment phase

At the clearing edge the number of recruits of each species surviving the dry season was positively correlated with seed size for both wind and animal dispersed species, although seed size accounted for only 27% of the variation in density of survivors of animal dispersed species (animal, $r^2 = 0.27$, F = 16.0, $P < 0.001$; wind, $r^2 = 0.73$, F = 13.4, $P < 0.05$)(Fig.5.9). In the clearing centres there was no such linear relationship.

There was a positive logarithmic relationship between relative survival success and seed size in both wind and animal dispersed species (Fig. 5.10). All recruits of species with seeds over 20 mm survived the dry season (i.e. *Helicia nilagirica*, *Castanopsis diversifolia*, *Beilschmiedia* sp. 1 and *Beilschmiedia* sp. 2). The coefficient of determination for animal dispersed seeds was much reduced by *Spondias axillaris,* which had poor survival (25%) for a species with a 20 mm seed. However, the measured dispersal unit of *Spondias* is a woody pyrene, which contains up to 5 much smaller actual seeds, so in this case the measured length was not a good indicator of the size of the embryo. When the outlying *Spondias axillaris* was removed r^2 was 0.69. At the lowest end of the size scale, all species with seeds 3 mm or smaller had under 35% survival (*Macaranga denticulata*, *Adinandra integerrima* and *Mallotus paniculatus*).

5.3.4 Seed trait based functional groups

The findings from the previous analyses were combined to generate three functional groups based on seed size, which best described observed colonization success in the clearing centres (Fig. 5.11).

Small-seeded species

Seeds under 2 mm dispersed abundantly into the clearing centre. This was true for both wind and animal dispersed seeds. No species with seeds under 2 mm recruited or established in the clearing centre

Medium-seeded species

Dispersal of seeds between 2 and 12 mm was highly variable for both wind and animal dispersed seeds, depending largely on the proximity of fruiting trees to the clearing edge. In the 2 – 12 mm range, wind dispersed species were more likely to reach the clearing centre (72 ± 15% chance) than animal dispersed species (21 ± 12% chance), mean of three sites. Survival was more closely linked to seed size than to dispersal group, although for a given seed size, survival of wind dispersed species was slightly lower.

Large-seeded species

There was no air-borne dispersal of seeds over 12 mm into the clearing centre. In the 2 – 12 mm range, where wind dispersed species recruited in the clearing centre, recruitment was < 3% of seed rain, but where animal dispersed species recruited, recruitment was 10 – 30% of seed rain. Recruitment of large-seeded species could not be assessed as there was no recorded seed rain. Within each species, percentage survival of the first dry season was generally very high.

The seed size distribution of all species recorded as seedlings at the start of the study (t0) supported the grouping described above (Fig. 5.12). The existing seedlings of small-seeded species in the clearing centres and edges suggested that these species could establish soon after disturbance. The presence of species up to 14 mm, suggested that the 12 mm limit observed during the study was subject to variation and that 14 mm might be a more accurate upper limit. However, any "limit" can only be interpreted as a guideline rather than an absolute barrier.

5.4 Discussion

5.4.1 Validity of the "filter" concept when applied to succession

It was originally intended to classify species according to their critical stage in the colonization of the clearing centre, according to the results obtained in the observational study. However results from the three replicate sites showed that the critical stage varied too much within species for this system to be valid. Despite this variability, the significant relationship between filter groups and seed size showed that the filtration of species during colonization was not entirely random, but was influenced by intrinsic species traits. Increasing seed size led to an decrease in the maximum potential density of dispersed seed and an increase in the survival of recruited seedlings during their first year. However, species would sometimes unpredictably disperse or establish below the maximum potential for their seed-size, leading to the between-site variations in critical stage. The factors responsible for such sub-optimal performance may have included stochastic events, site factors and sampling error; the latter two are discussed later.

5.4.2 Seed size vs. colonization

The results presented here correspond with other studies which have shown that seed rain abundance is negatively related to seed size (Pianka, 1970; McClanahan and Wolfe, 1993). Seeds of up to 12 mm were dispersed to the clearing centre during the period of observation, while established seedlings suggested a maximum dispersal limit of 14 mm. Most other studies have suggested upper seed-size limits which are smaller than or very similar to the results of this study. In abandoned Amazonian pasture, da Silva *et al.* (1996) extracted seeds of up to 13 mm from bird faeces, while Nepstad *et al.* (1996) found seeds of up to 16 mg, a dry mass comparable to that of *Macaranga denticulata*, which has a dry mass of c. 21 mg and is only 2.4 mm in length. McClanahan and Wolfe (1993) found seeds of 159 mg (similar to *Prunus cerasoides*, 170 mg and 9.7 mm) in seed traps on a reclaimed mine site in Florida. Ganzhorn *et al.* (1999) suggested that only one vertebrate species dry deciduous forest in Madagascar was able to pass seeds of >11 mm long through its digestive tract unharmed. One study (Parrotta *et al.*, 1997) found evidence of dispersal of much larger seeds: species with seeds over 25 mm were found to have colonized reforestation plots. However, this may have involved dispersal by mammals, of which there were a full complement of large dispersers (e.g. tapirs – *Tapirus* spp.) and this site had been undisturbed for ten years, allowing plenty of time for rare dispersal events.

The larger estimates can be considered to be more conservative as they predict that a smaller percentage of species in the tree community will be excluded from colonizing clearings. None of the comparable studies showed dispersal of seeds larger than that found in this study

The net result of the negative effect of seed size on dispersal and its positive effect on establishment is demonstrated by comparing the seed-size distribution of survivors in the clearing edge with that in the clearing centre. At the edge, where proximity to the forest reduces the advantage of seed mobility, the larger seeded species are better represented due to their higher levels of recruitment and survival. In the centre though, the higher recruitment and survival is offset by lower seed dispersal and it is the species with medium sized seeds which are most prolific, while the very small and very large species are absent.

So the net effects of filtration during clearing colonization are predictable only for species at each end of the size spectrum, where an upper size limit to seed dispersal exists. In between these limits no seed-size has an overall advantage. These data support the theory that if the animal vectors of the largest species are present [so there is no upper size limit to dispersal], then seed size does not necessarily predict colonizing ability (Howe and Smallwood, 1982). For example, Davis used pollen records to show that both Picea, with seeds of 0.002 g and Quercus, with seeds of 1 to 3 g colonized America after glacial retreat at rates of at least 250 m per year. However, this theory is not supported by Wunderle (1997) who states that even when a full compliment of native seed dispersers are present the dispersal rate of large-seeded species may be low enough to warrant human intervention to provide "adequate dispersal".

5.4.3 Importance of environmental factors on the colonization process

Species density declined during clearing colonization due a process of filtration whereby individual seeds or seedlings were eliminated at each stage of colonization. However, the filtration effect cannot be attributed solely to factors relating to clearing colonization, as species density also declined in the forest during recruitment and first year seedling survival. This was expected as it is an intrinsic characteristic of the regeneration phenomenon that the number of individuals declines during each phase of regeneration (Alvarez-Bullya, 1992). Some insight may be gained into the role of clearing colonization in depleting species density by comparing the relative loss at each stage in the clearing with the loss in the forest and by comparing the filtration process at one site with another.

In each unit area of 1 m^2, fewer species established in the clearing than in the forest. This was due primarily due to the filtering effect of seed dispersal reducing the initial seed pool rather than any difference in species loss during seedling recruitment or survival of the first dry season. In both the forest and the clearing zones the recruitment phase was the most powerful filter in that it accounted for the greatest reduction of species in each unit area.

Recruitment consistently accounted for the highest level of species loss in the forest as well as in the clearing. As the degree of filtration was the same in all zones and all sites, little insight can be gained from these data into the nature of the environmental filters at work. The highly uniform results suggests that limiting factors were intrinsic to the species themselves, for example seed viability, rather than environmental, which would have been expected to give more variable results. Recruitment as defined here encompasses two distinct phases, seed germination and survival and growth of the germinants to 5cm. It is possible any environment-related variability in the success of each phase was masked by pooling them together.

The probability of success at each stage was related to seed size. However, success at each stage was variable within each group as it was strongly influenced by random external factors such as tree proximity, site vegetation structure, unpredictable behaviour by animal vectors and predators, wind direction, flooding, fire, human interference, surrounding vegetation growth and collapse etc, etc. Thus it is impossible to predict with certainty that a species in a certain group will definitely behave in a certain way. Environmental factors which may have influenced the probability of colonization are now discussed.

Prominent trees. — Seed size placed a limit on the potential abundance of seed in the seed rain, but below this limit, seed density was unpredictable for a particular species. At first it was thought that the high variation was due to differences in the amount of available seed in the forest. If this were the case, then it would be expected that the measurement of relative dispersal success (that is the ratio of seed in the clearing to seeds in the forest) would give less variable results (Fig. 5.6) and would perhaps be more closely linked to seed size. This was not the case. Dispersal success appeared to be governed simply by the proximity of single fruiting trees to the clearing edge rather than the overall abundance of trees in the forest.

The seed rain was particularly poor at Site 3, where species density was only 20% that of the forest. Two factors may account for this high level of filtration.

Forest fragmentation. — Firstly, the clearing at Site 3 was situated in a more fragmented forest environment than the clearings as Sites 1 and 2. Although the seed rain in the remaining mature forest was equivalent to the other two Sites, (Fig. 5.2), the forest bordered the clearing at Site 3 on only two sides, compared with three sides at Site 1 and four sides at Site 2. Thus the forest-clearing interface was relatively restricted at Site 3.

Perches. — Secondly, the vegetation structure at Site 3 was primarily grass and ferns, in contrast to Sites 1 and 2 which were dominated by shrubs and ferns (Chapter 2). An increasing body of work predicts that shrubby vegetation will facilitate seed dispersal in clearings through the provision of perches and roosting sites for birds and bats acting as seed vectors (e.g. da Silva *et al.*, 1996).. MacArthur et al (1961 # 2441) bird diversity with structural divers

Fire. — Fire may account for the failure of the animal dispersed component of the seed rain to recruit at Site 3. Eight out of the 12 animal dispersed species in the clearing seed rain had a delayed rainy dispersal syndrome and consequently dispersed all their seeds before the fire in March 1995. It is likely that the seeds of these species were destroyed when the site burnt. Forest burning reduces the seed bank size, Ewel *et al.* (1981), Uhl *et al.*. (1981) and many forest species from Doi Suthep-Pui National Park have been shown to be killed by burning at temperatures typical of a forest fire (Hardwick *et al*, 1992). However, recruitment levels were not high at any site and five of those eight delayed rainy species also failed to recruit at the sites which were not burnt.

The other four animal dispersed species in the seed rain (*Debregeasia longifolia*, *Eurya acumminata*, *Symplocos macrophylla* and *Trema orientalis*) also failed to recruit at all sites. For these mostly small-seeded species (0.5, 1, 6.5 and 2.5 mm respectively), burning of seeds was definitely not a factor in the recruitment failure, as all had intermediate dry or rapid rainy germination syndromes, with seed dispersal occurring (and usually peaking) after the fire.

The only animal dispersed species to recruit seedlings in the clearing were *Spondias axillaris*, *Prunus cerasoides* and *Macaranga denticulata*, species that had not been recorded in the seed rain in the zones where they were recruiting. This apparent absence from the seed rain could, of course, have been due to sampling error. However, even if the seeds had been dispersed aerially to the clearing they would probably have been lost in the fire, as both were delayed rainy species which dispersed their seed several months before the fire. A possible explanation for the anomalous recruitment of these species is that the seeds were present in the soil seed bank during the fire and survived the heat through being buried in the soil. *Macaranga denticulata* is a typical "pioneer" species which is known to be present in the soil seed bank in montane forest in northern Thailand (Cheke *et al.*. 1979). Another possible explanation is that the seeds arrived in the clearing via secondary dispersal after the fire.

5.5 Conclusion

- On the basis of seed size and dispersal method, species can be divided into three functional groups, characterised by different critical stages.
- In this study, small-seeded species (with seeds less than 2 mm long) dispersed prolifically to the clearings but failed to recruit seedlings of 5 cm or more. Colonization may be restricted to a very short window of opportunity immediately after disturbance, before competing herbs and shrubs take over and to isolated patches of bare soil within shrubby areas.
- Medium-seeded species have no consistent critical stage. The filtering process of colonization is different for those dispersed by wind and animals. Recruitment was an inhibiting stage for wind dispersed species. Dispersal and recruitment were inhibiting stages for animal dispersed species. Colonization by species with medium sized seeds was heavily dependent on the presence of fruiting trees at the clearing edge.
- For large-seeded species, the critical stage was dispersal. There was no evidence of dispersal by birds or bats of seeds over 14 mm long. Scatter-hoarding of large seeds by small mammals was mostly restricted to the edges of the clearings. Thus colonization of shrubby clearings is thus largely restricted to species with medium sized seeds of between 2 and 14 mm.
- The proposed functional groups indicate the probability that a species will colonize an old abandoned agricultural clearings and the stage at which it is most likely to be filtered out. However, there is variation with the groups, particularly within the medium-seeded group. among sites.
- Further research is needed to determine what traits other than seed size and dispersal mode predict a species colonization ability and limiting stages.

lead on to next chapter

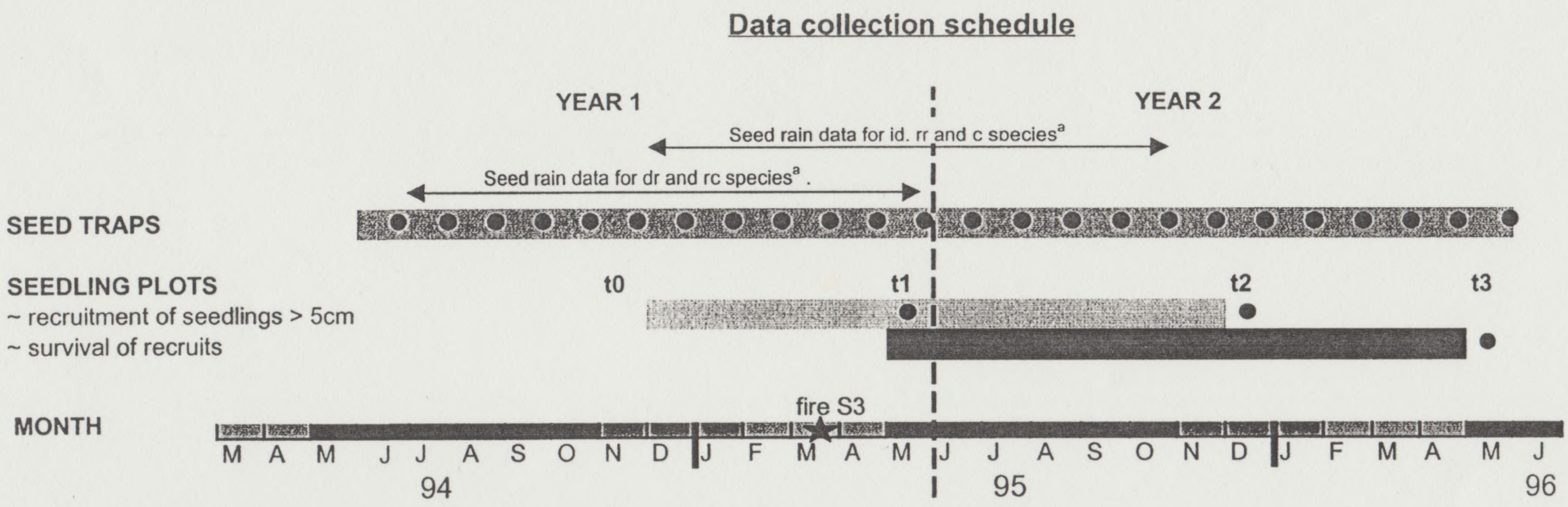


Fig. 5.0. Data collection schedule. Each black spot represents one data collection occasion. The period of seed rain data was selected for each species according to germination syndrome, in order that the data would correspond with the oberved seedling establishment during the growing season of 1995. Germination syndromes (based on Garwood, 1983) are abbreviated as follows: dr = delayed rainy, rc = rapid rainy (late), id = intermediate dry, rr = rapid rainy (early), c = continuous. The dark blue strip above the data axis from May to October represents the rainy season.

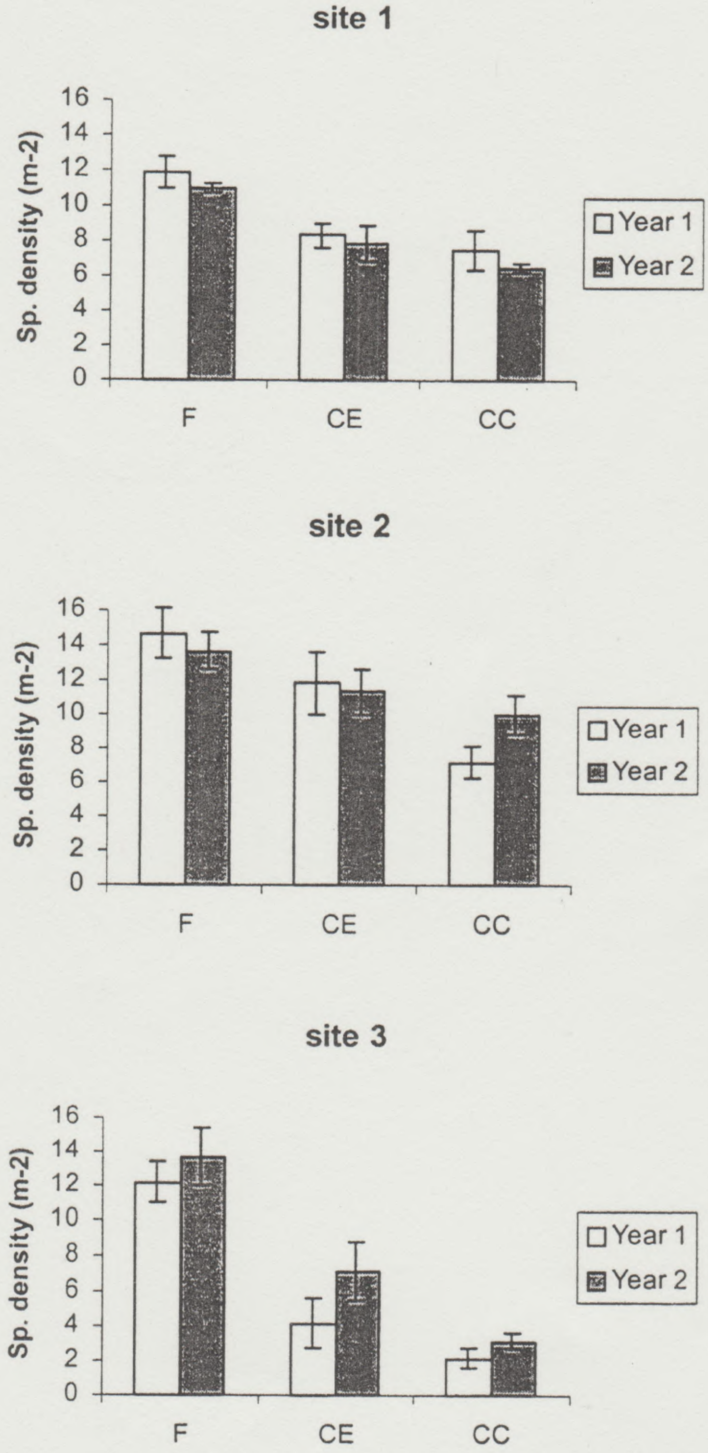


Fig. 5.1. Species density of seed rain by site, zone and year (mean number of species per 1m2 seed trap over one year, mean and standard error of six traps.

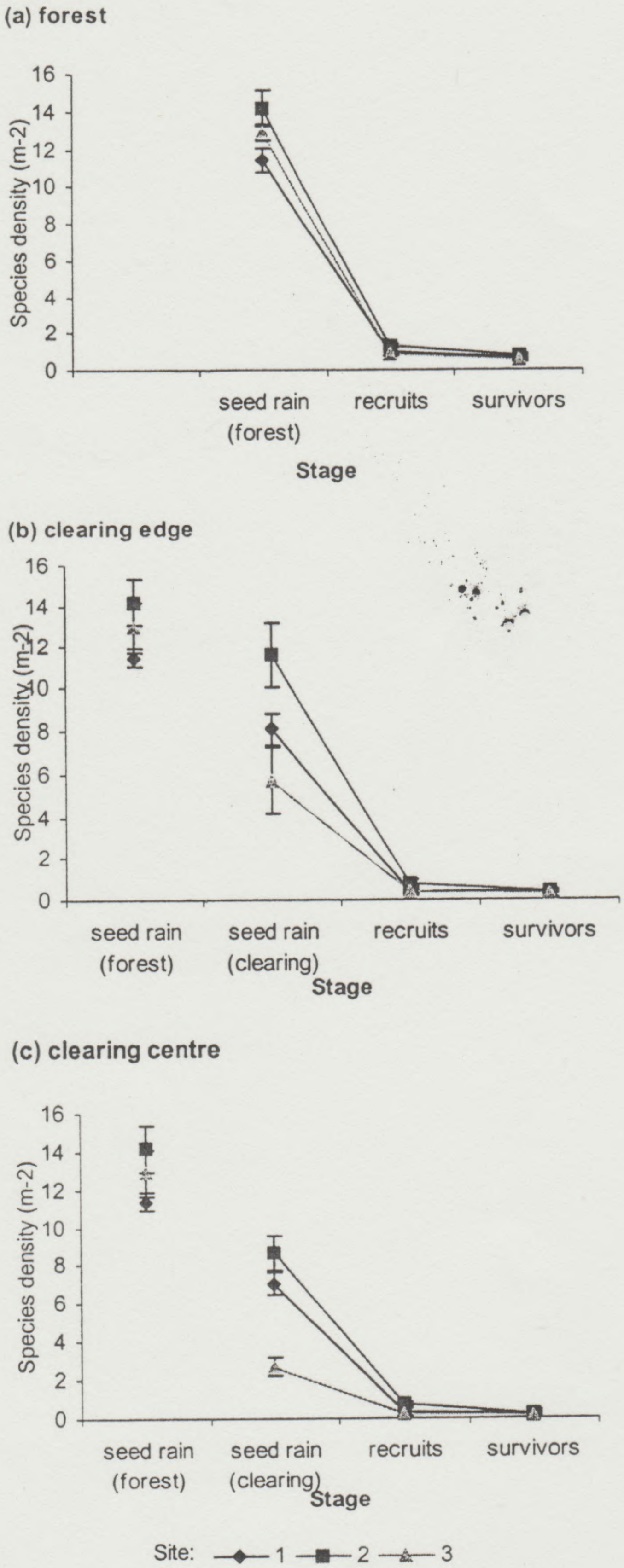


Fig. 5.2. Tree species density by static life-cycle stage in: (a) forest, (b) clearing edge and (c) clearing centre. Species density is the number of tree species recorded per m2 at each stage of one years' recruitment process. Values are mean and standard deviation of six plots. Recruits are newly recruited seedlings over 5 cm high. Survivors are recruits surviving to the end of the first dry season.

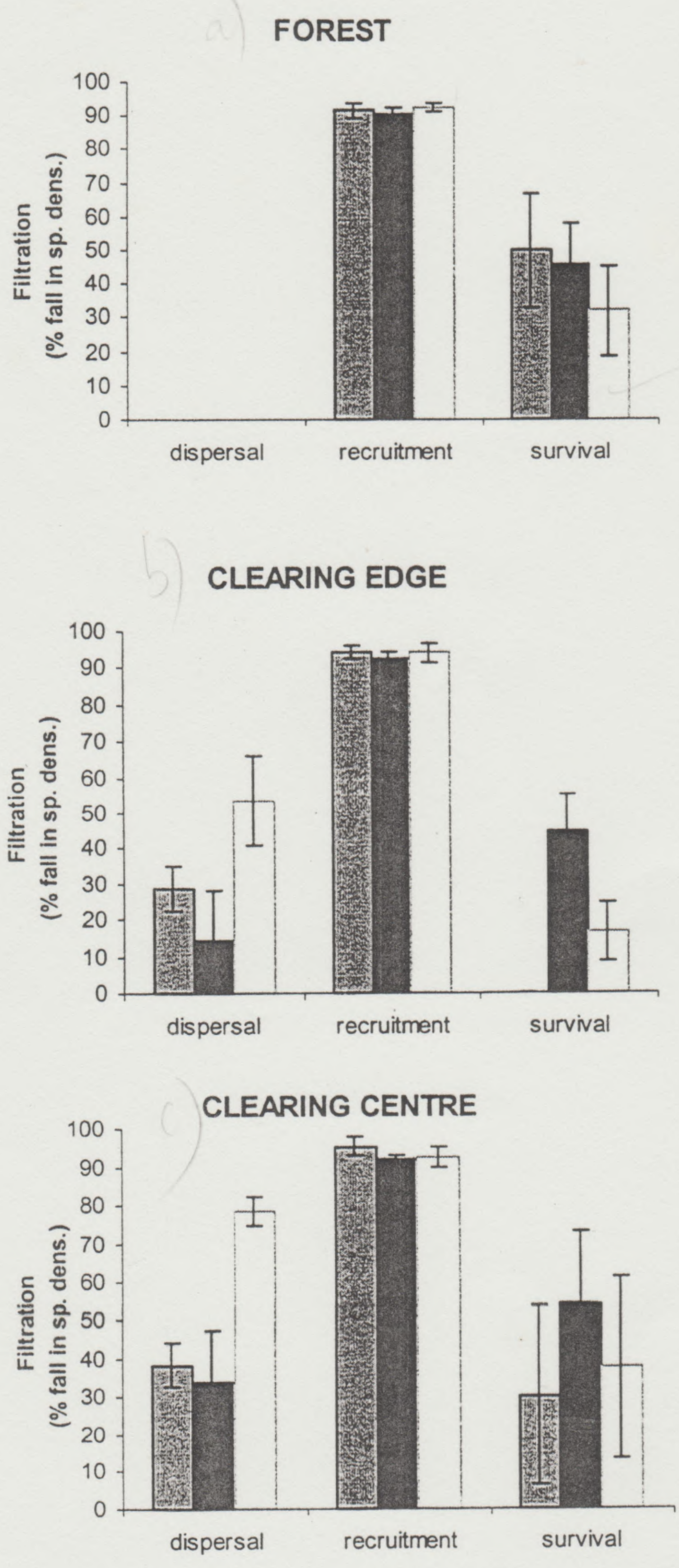


Fig. 5.3. Degree of filtration of tree species, shown as % fall in species density, by life-cycle stage during one annual cycle of the regeneration / colonisation cycle in (a) forest, (b) clearing edge and (c) clearing centre.

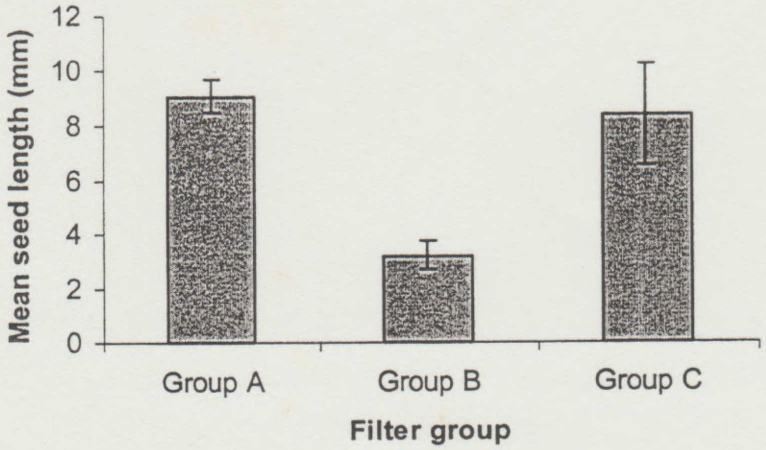
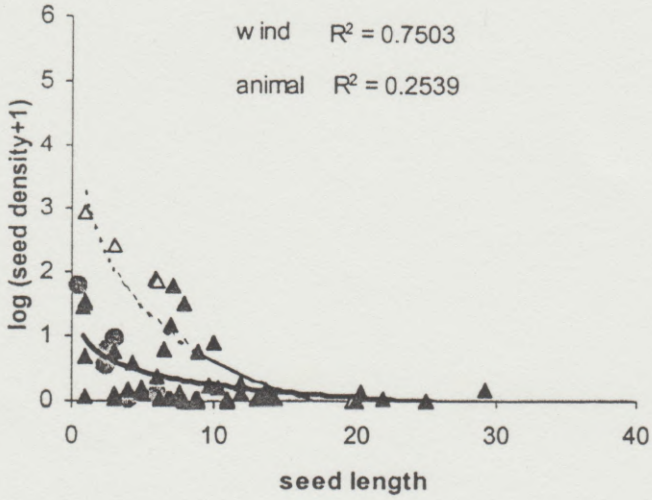
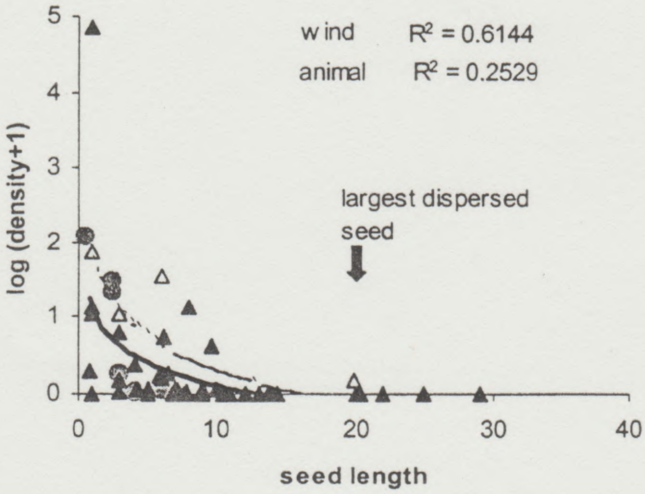


Fig. 5.4. Mean seed size of trees species in each filter group. Each column is mean and standard error of three sites.



(b) Clearing edge



(c) Clearing centre

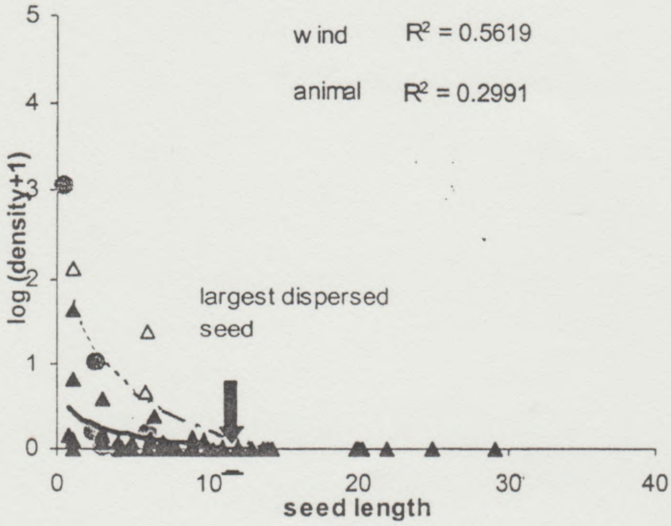


Fig. 5.5. Density of tree seeds (m2) as a function of seed size in (a) forest, (b) clearing edge and (c) clearing centre. Each point represents one species. The density was determined by summing the number of seeds of each species trapped during one annual regeneration cycle. Damaged and semi-predated seeds were included in the total but obviously immature seeds were excluded.

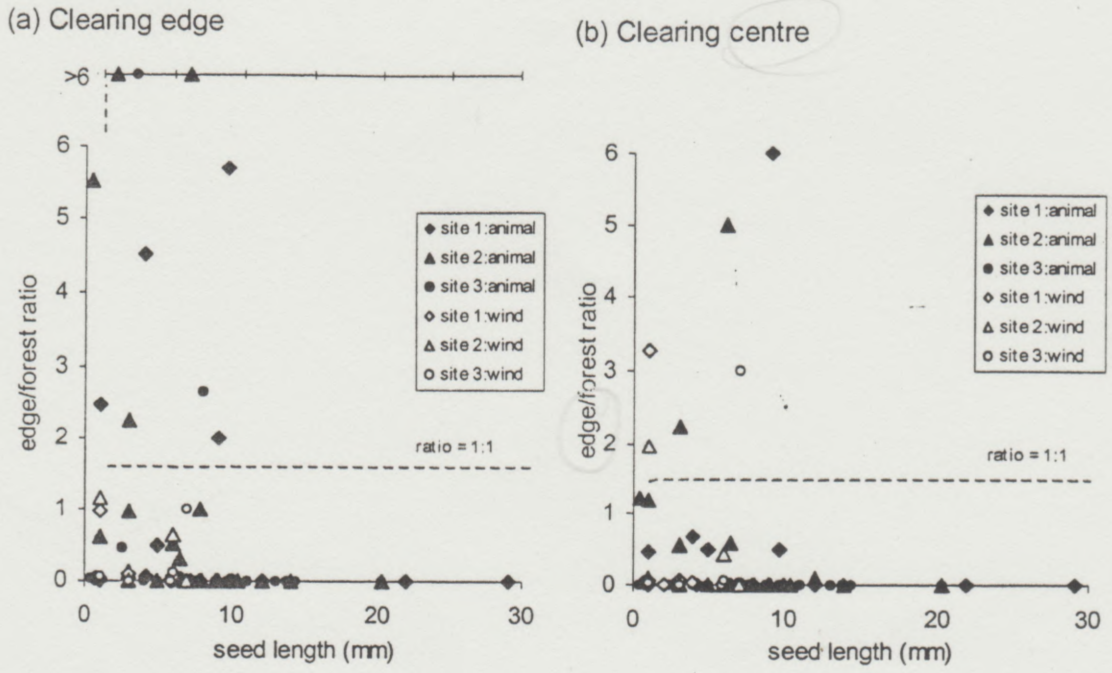
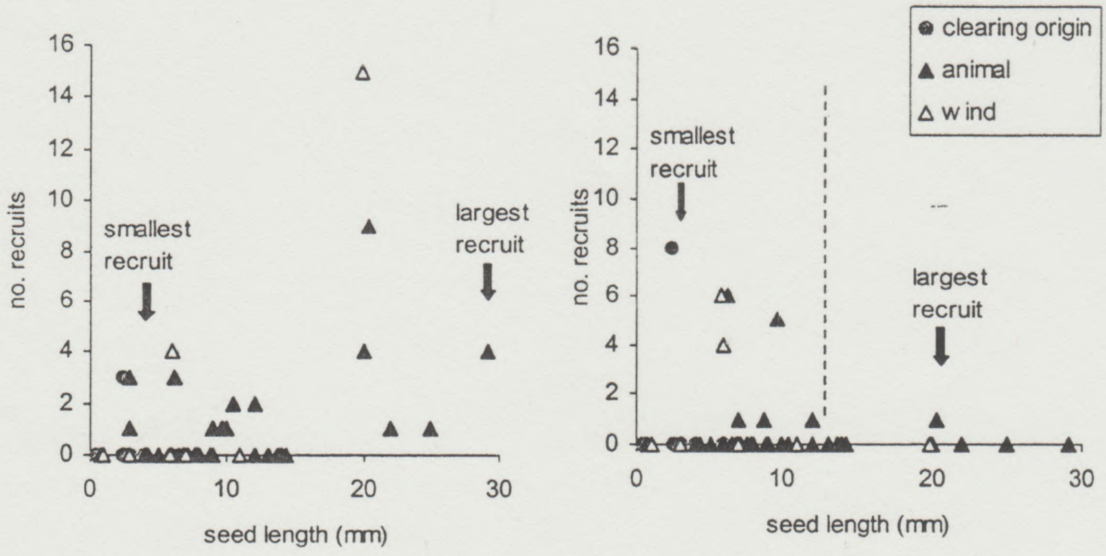


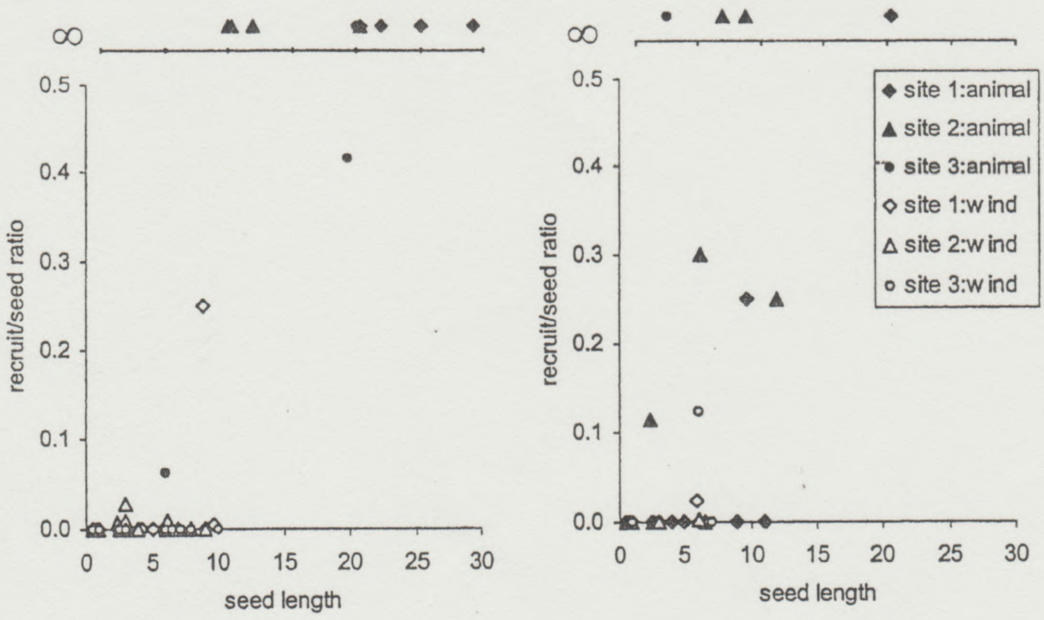
Fig. 5.6. Estimated dispersal success of tree seeds (ratio of seed density in clearing seed rain to seed density in adjacent forest seed rain) as a function of seed size in (a) clearing edges and (b) clearing centres. Results are shown separately for each site. Each point represents a single species in the forest seed rain at one site. Species which fruited in the clearing at a particular site are not included. The density was determined by summing the number of seeds produced in one annual regeneration cycle. In the clearing edge zones, three species had extremely high ratios. Site 2: Ficus superba (seed = 1 mm, ratio = 1951:1), Mischocarpus pentapetalus (seed = 6.2 mm, ratio = 84:1). Site 3: Macaranga denticulata (seed = 2.4 mm, ratio = 139:1).



a) Clearing edge

b) Clearing centre

Fig. 5.7. Density of newly recruited tree seedlings, at least 5 cm high, in (a) clearing edge and (b) clearing centre as a function of seed length. Each data point represents the number of recruits of a single species from the three sites is combined. Solid triangles: animal dispersed species of forest origin. White triangle: win dispersed species of forest origin. Green (grey) circles: species fruiting in some clearings (all bird dispersed)



a) Clearing edge

b) Clearing centre

Fig. 5.8. Estimated recruitment success of tree species (ratio of density of recruits in the clearing to density of seeds in the clearing seed rain) as a function of seed size in (a) clearing edges and (b) clearing centres. Results are shown separately for each site and for wind and animal dispersed species. Each point represents a single species in the clearing seed rain at a single site. All identified tree species are included, except agricultural crops (e.g. coffee). Species which recruited seedlings but were not present in the seed rain have a success ratio of ∞ .

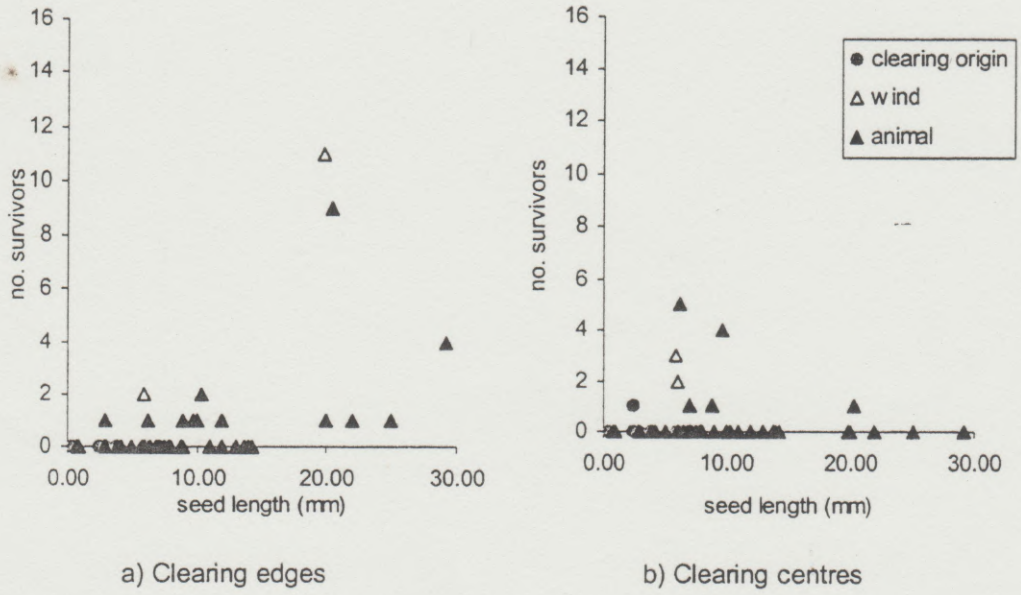


Fig. 5.9. Density of recruits surviving the first hot season, in (a) clearing edge and (b) clearing centre as a function of seed length. Each data point represents the total number of survivors of each species from the three sites combined. Solid triangles: animal dispersed species of forest origin. White triangle: win dispersed species of forest origin. Green circles: species fruiting in some clearings.

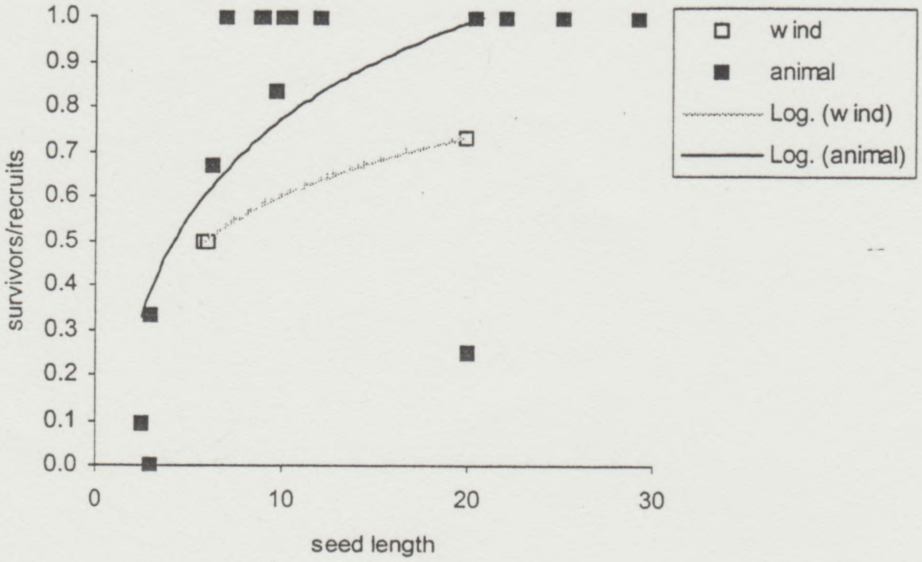
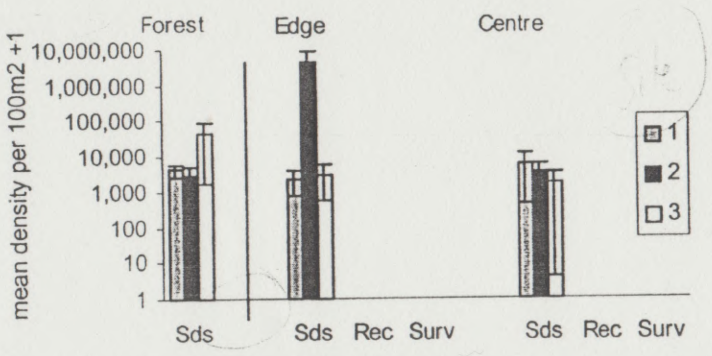
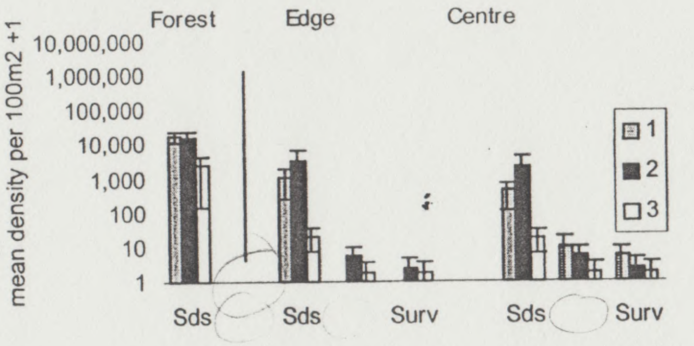


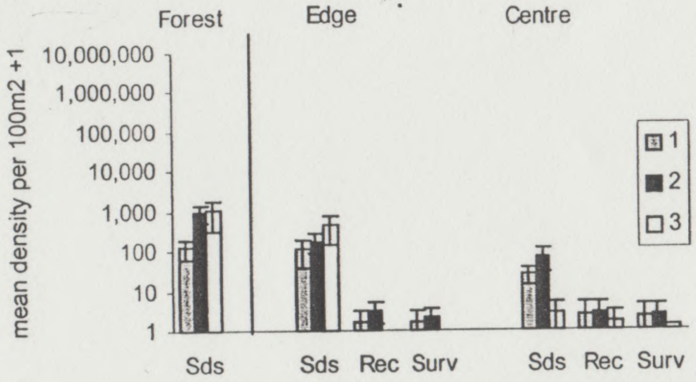
Fig. 5.10. Survival success of tree species (ratio of number of clearing recruits surviving the first dry season to number of recruits at the beginning of the dry season), as a function of seed size. Each point represents a single species, with data pooled from the clearing edges and clearing centres in three sites. Survival was calculated for all recruits present at the beginning of the cold dry season in December, 1995. Data include all identified tree species except agricultural crops. Wind dispersed species: n = 3, r2 = 0.99. Animal dispersed species: n = 16, r2 = 0.43.



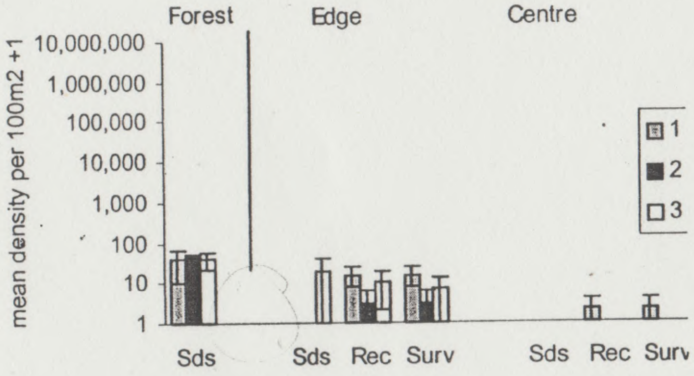
a) Small seeded species



b) Medium-seeded, wind dispersed species



c) Medium-seeded, animal dispersed species



d) Large-seeded species

Fig. 5.11. Density of seeds or seedlings per 100 m2 at each stage of the colonisation process for (a) small seeded species, (b) medium sized wind dispersed species, (c) medium sized animal dispersed species, (d) large seeded species. Sds = seeds in the seed rain, Rec = total number of seedlings at least 5 cm high recruited during the rainy season; Surv = number of surviving recruits at the end of the following dry season. Data is shown for each site.

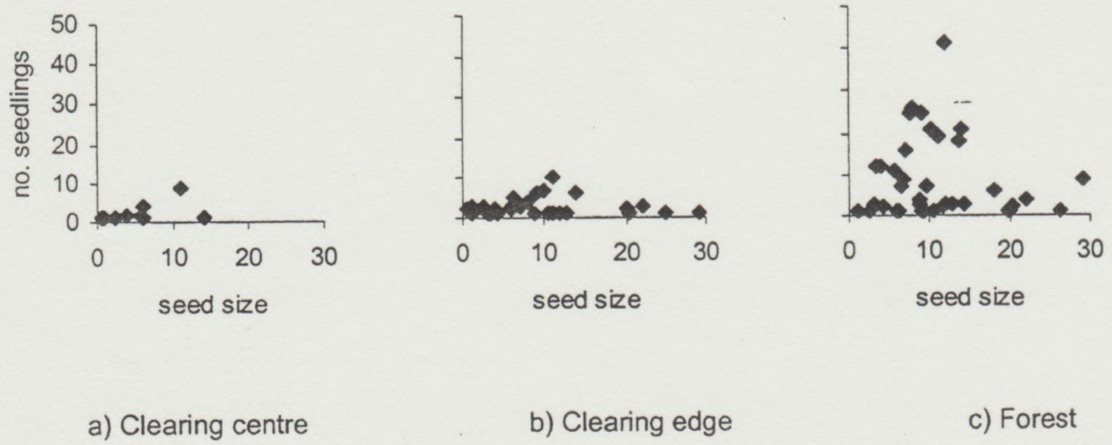


Fig. 5.12. Distribution of seedlings at t0 by seed size: in a) clearing centres, b) clearing edges and c) forests. Data points are total number of seedlings from three sites pooled.