

CHAPTER 4

SEED PRODUCTION

4.1 Introduction

Clearings resulting from decades of burning and agriculture are likely to lack woody plants (whether from sprout or seed origin) or a soil seed bank, so the succession process will depend entirely on the incoming seed rain (Nepstad *et al.*, 1996). Where the seed rain is the only source of regenerative material, any factors that limit it will impose a major block on the regeneration process.

Differences in temporal fruiting patterns between species will affect the availability of seed throughout the year. Most recent studies on the ecology of fruit production in the seasonal tropics focus on the seasonal phenology of fruit production. The seasonality of a species' fruit maturation can often be predicted from its dispersal mode. Wind dispersed species ripen and disseminate fruit in the dry season, peaking in the latter half (e.g. Frankie *et al.*, 1974; Foster, 1982; Guevara de Lampe *et al.* 1992; Elliott *et al.*, 1994). In contrast, fruit maturation in fleshy, animal dispersed species tends to occur continuously with a peak in the rainy season (e.g. Lieberman, 1982; Elliott *et al.*, 1994; Guevara de Lampe *et al.*, 1992), with some studies showing a second peak at the end of the dry season (e.g. Foster, 1982). An exception to this general pattern has been observed in the seasonally dry forests of western Costa Rica, where there is a unimodal fruiting peak for all species at the end of the dry season (Daubenmire, 1972 and Frankie *et al.*, 1974).

Fewer studies have concentrated on the inter-annual fruiting patterns of different species and ecological guilds, an issue of particular relevance to ANR, as the natural colonisation process can only be accelerated if seed is available. Most of these studies assessed the fruit crop as a source of food for frugivores (e.g. Terborgh, 1983; Newton, 1988) rather than as a source of seed for the colonisation of deforested areas.

Newstrom *et al.* (1994) reviewed existing classification systems for flowering patterns in tropical forests and proposed a new system, which can equally be applied to fruiting patterns. Their system is based on graphical representation of four basic flowering patterns: continual, sub-annual, annual and supra-annual. An important aspect of their approach is the separation of different levels of analysis: individual, population, guild and community. For predicting the seed availability of a particular species, fruiting patterns at the population level are most relevant.

Janzen (1978) has provided the most thorough treatment of variability in fruit production and its causes and implications. Drawing on at least five years of data from well replicated samples of individual species in Costa Rica, he categorised species according to the frequency and synchrony of fruiting of individual trees. The implications for fruit availability at the population level are as follows:

- **Annual fruit availability.** Two of Janzen's fruiting patterns result in annual availability of fruit at the population level: (1) annual fruiting by all trees; (2) unsynchronised supra-annual fruiting. In the latter, individual trees skip years between fruiting events, but as the periodic fruiting events of individual trees are unsynchronised, fruit is available at the population level every year. Species in both these classes produce fruit every year, but the two classes differ in the proportion of the population producing fruit in any one year.
- **Supra-annual fruit availability (mast fruiting).** Janzen's synchronised supra-annual fruiting pattern results in a complete lack of fruit availability in some years. This may happen because all trees belong to a same-aged cohort and thus start fruiting at the same time (semelparous behaviour), but more commonly, because all trees fruit periodically at the same time in response to the same weather cue (iteroparous behaviour).

A few authors have investigated the spatial and temporal variation in fruit abundance within individual species. Levey (1990) studied the effect of habitat on fruiting in *Miconia centrodesma*. He showed that the high-light conditions in gaps enabled trees to produce larger fruit crops, which extended over longer periods than trees in the understorey. Ghazoul *et al.*, (1998), showed that fruit set in *Shorea siamensis* was dependent on tree density. When tree density was decreased by disturbance, inter-tree movements of the pollinating *Trigona* bee declined, leading to an increase in inbred fruit which aborted before maturity, thus lowering fruit set. Owens (1995) considered constraints to seed production in tropical trees from a biological perspective and showed that constraints may operate at all stages of the seed production process from floral initiation through to fruit maturation.

4.1.2 Objectives

The overall objective of this chapter is to find out whether low fruit production could be a factor limiting seed input into abandoned agricultural clearings. If so, then a further objective will be to determine why some species fail to produce fruit and which species are most likely to be limited in this way.

Specific questions are:

- Each year, what percentage of common species in the forest adjacent to each clearing failed to produce fruit?
- Does fruit production vary between sites or forest zones?
- What factors limit fruit production?
- What species characteristics are related to fruit production?

4.2 Methods

4.2.1 Terminology

The terminology in this section generally follows Newstrom *et al.* (1994).

The presence of ripe fruit was interpreted as the presence of seed. However, ovule and embryo abortion may lead to a lack of viable seed within healthy-looking mature fruit (Owens, 1995). This could not be detected by the fruit availability survey but did become evident in the germination experiments (Chapter 6), which indicated that although a proportion of fruits may have contained non-viable seeds, no case was observed where the entire fruit crop was non-viable.

Potential
Actual see sub 4.2

4.2.2 Sample plots

In order to record fruiting phenology sample plots were established in the forest adjacent to the clearing in each of the three study sites (more detailed site descriptions are given in Chapter 2). Circular plots, 10 m in diameter, were placed adjacent to the clearing's edge and spaced 20 m apart around the clearing unless one happened to fall in a place with no trees, in which case it was moved forward until it lay entirely within an area with trees (Table 4.1). Owing to the varying layout of the forest at each site, the forest edge plots were located in forest on three sides of the clearing at Site 1, two sides at Site 2 and two sides at Site 3. A second set of inner forest plots were arranged in the same way, deeper inside the forest between 10 m and 100 m from the edge. Within each plot, all trees with a girth at breast height (GBH) of 10 cm or more (diameter at breast height ≥ 3.2 cm) were tagged, identified and their GBH was measured. This lower size limit is lower than is commonly used, in order to ensure that the smallest mature fruiting trees were not missed, thus ensuring that the fruiting abundance of their species was not underestimated.

Table 4.1. Layout of plots to survey monthly fruit abundance (put in mean tree densities):

	Edge plots	Inner plots	Total
Site 1	12	12	24
Site 2	6	12	18
Site 3	6	12	18
Total	24	36	60

4.2.3 Scoring reproduction

The abundance of flower buds, flowers, ripe and unripe fruit was monitored at monthly intervals for two years, from June 1994 until May 1996. Each state was scored for each tree using the crown density method derived from the system conceived by Keolmeyer (1959). A linear scale of 0 to 4 points was used, with 4, 3, 2 and 1 representing 100%, 75%, 50% and 25% canopy coverage respectively. 0.5 represented a tiny amount, well below 25% coverage. Fruit

ripeness was judged by colour, size, texture of embryo, dehiscence of fruit, abundance of fruit fall and any other characteristic known to be appropriate for a particular species.

4.2.4 Estimating maturity

In many species in the plots, maturity was clearly size-dependent. Trees under a particular GBH showed no reproductive behaviour of any kind, while trees above this size would demonstrate at least sporadic reproductive behaviour, either fruiting, or flowering for a brief period if they failed to fruit. However, in four species (*Elaeocarpus floribundus*, *Lithocarpus elegans*, *Phoebe lanceolata* and *Phoebe cathia*) trees in the plots that were clearly large enough to be mature failed to show any reproductive behaviour at all. For these species, maturity was estimated by comparing the GBH with mature fruiting trees of the same species, genus or family, found outside the plots.

4.2.5 Analysis of results

The amplitude of a fruiting episode of an individual tree was represented by the "peak fruit score" - the unripe fruit score recorded the month before ripe fruit was first observed. This was used in preference to the highest total fruit score, which may have included immature fruit that subsequently abscised before reaching maturity (Owens, 1995) or to the highest ripe fruit score, which may have been recorded after fruit had already started to be disseminated.

The relative availability of fruit of a particular species was represented by the Fruit Availability Index (FAI), calculated as follows:

$$\text{FAI} = \frac{\sum \text{peak fruit scores}}{4} \times \frac{1}{\sum \text{plot area (ha)}}$$

The FAI represents the equivalent number of fully fruiting trees per hectare, derived by dividing the total score for all trees by the maximum score of four. This assumes that the fruiting scores are additive, e.g. that two half fruiting trees scoring 2 are equivalent to one fully fruiting tree scoring 4. This index is an attempt to solve the dilemma (posed by Janzen, 1984) of combining both tree and fruit abundance. It also provides a measurement of relative fruit abundance, which is meaningful for different species, irrespective of seed size and for different sites, irrespective of total plot area. The effect of tree size should be considered when interpreting the results, but was not included in the index as the exact nature of the relationship between tree size and fruit abundance is not known and may vary between species.

The data were grouped in different ways to answer different questions and a summary of the groupings is presented in Table 4.2.

Table 4.2. Grouping of data for analysis

Group	Criteria	
	Three sites combined	Individual sites
1. POTENTIAL SEED SOURCE		
1.1 All trees (with GBH ≥ 10 cm)		
a) All species	All species present in plots at start of study (n=106)	
b) Common species	Species represented by at least five trees in plots at start of study (n=27)	
c) Site-dominant species		At each site, species with density of at least 25 trees ha ⁻¹
1.2 Mature trees only		
a) All species	All mature trees in plots	
b) Common species	Common species represented by at least four mature trees in plots (n=19).	
2. ACTUAL SEED SOURCE		
2.1 Fruiting species	All species with fruiting trees in at least one year (n=47)	
2.2 Fruiting trees only	All fruiting trees in each year separately	

Differences in annual fruit production (all species combined) between sites and zones were compared using the density of fruiting trees per plot (Table 4.2, group 2.2) and the mean peak fruit score per mature tree (Table 4.2, group 1.2a) per plot as variables. Each variable was then tested in a two-way ANOVA, using each plot as a unit and site and zone as factors.

To increase sample sizes per species, differences between species were analysed using trees pooled from the three sites. Further analysis focused on the 27 most common species, represented by at least five trees (Table 4.2, group 1.1c).

To assess the extent to which species fulfilled their fruiting potential, the annual mean peak fruit score was calculated for the 19 common species represented by at least four mature trees (Table 4.2, group 1.2b). Immature trees were eliminated from the calculation to avoid confusing fruiting success with population structure.

Diagnosis of the frequency of fruit production was restricted to the 19 common species represented by at least 4 mature trees (Table 4.2, group 1.2b). Following the classification system presented in the introduction, fruit availability of a species was considered "annual at the population level" if fruit were produced in both years (even by different trees) and "supra-annual at the population level" if fruit were produced in only one or neither year.

The effect of population structure on fruit production, was analysed for the 27 commonest species (Table 4.2, group 1.1b). Species were classed as either fruiting (i.e. at least one tree

producing fruit) or non-fruiting and the density of mature trees was compared between the two groups using a Kruskal-Wallis test as the data failed to meet the requirements of ANOVA.

4.3 Results

4.3.1 Potential seed source

In the survey of all trees in the potential seed source (Table 4.2, group 1.1a), 106 tree species were found in the three sites (Appendix I). Of these, 88 were identified to species, five to genus, four to family and nine were unidentified. Although only 83% of the species were fully identified, they accounted for 93% of all trees, as most of the unidentified species were relatively rare.

The sites were considered to be independent replicates of evergreen forest (Maxwell, 1988). Species of Fagaceae, Theaceae and Lauraceae were common at all sites, although the most dominant species varied between sites (Chapter 2). When trees from all sites were pooled, there were 27 "common" species (Table 4.3), represented by 5 or more trees at the start of the study (Table 4.2, group 1.1b). Of the common species, 89% were found at two or more sites.

4.3.2 Actual seed source

4.3.2.1 Species composition

Of the potential seed source of 106 species, 47 fruited during the study period (Table 4.2, group 2.1a). Of these, six species were common to all three sites (*Eurya acumminata*, *Helicia nilagirica*, *Saurauia roxburghii*, *Styrax benzoides*, *Vernonia volkameriifolia* and *Wendlandia scabra*) and ten were found at two sites. Thirty-one fruiting trees were unique to one site, although 19 of these were represented by a single fruiting tree. Thus, the composition of fruiting species differed between the three sites although the number of fruiting species per site (23) was the same.

The composition of fruiting species in the forest edge zones was different to that in the inner forest zones (Fig. 4.1) although again, this was strongly influenced by the high proportion of fruiting species represented by a single tree (26% to 40% of fruiting species per site per year). The differences in species composition appeared random: no well represented species were consistently restricted to either edge or inner forest zones.

Table 4.3. Details of the 27 most abundant species in the tree plots combined

Species	N ^a		No. mature trees ^b		FAI ^c		Population level fruit availability ^d
	Yr 1	Yr 2	Yr 1	Yr 2	Yr 1	Yr 2	
<i>Castanopsis diversifolia</i>	56	54	6	6	5	0	supra-annual
<i>Styrax benzoides</i>	34	33	22	21	23	6	annual
<i>Vernonia volkameriifolia</i>	31	31	31	31	39	38	annual
<i>Wendlandia scabra</i>	21	19	11	11	5	16	annual
<i>Saurauia roxburghii</i>	20	18	19	18	26	25	annual
<i>Schima wallichii</i>	18	18	6	6	6	4	annual
<i>Eurya acuminata</i>	17	14	13	13	12	10	annual
<i>Helicia nilagirica</i>	17	17	13	13	10	5	annual
<i>Castanopsis tribuloides</i>	16	15	4	4	7	5	annual
<i>Castanopsis acuminatissima</i>	16	15	8	8	7	7	annual
<i>Lithocarpus elegans</i>	15	14	1	1	0	0	
<i>Engelhardia spicata</i>	14	14	5	5	3	3	annual
<i>Phoebe lanceolata</i>	14	12	4	4	0	0	supra-annual
<i>Acronychia pedunculata</i>	11	10	9	8	16	11	annual
<i>Beilschmiedia sp. 1</i>	10	10	4	4	6	0	supra-annual
<i>Litsea salicifolia</i>	9	6	6	4	1	2	annual
<i>Heliciopsis terminalis</i>	9	9	4	4	0	0	supra-annual
<i>Glochidion acuminatum</i>	9	9	7	7	5	4	annual
<i>Cinnamomum iners</i>	8	8	1	1	2	2	?
<i>Phoebe sp. 1</i>	7	7	1	1	0	1	?
<i>Elaeocarpus floribundus</i>	6	5	1	1	0	0	?
<i>Eugenia albiflora</i>	6	6	2	2	0	2	?
<i>Artocarpus lanceolata</i>	6	6	0	0	0	0	?
<i>Rhus chinensis</i>	5	3	4	3	0	0	annual (shade intolerant)
<i>Erythrina stricta</i>	5	5	3	3	2	0	?
<i>Spondias axillaris</i>	5	5	4	4	3	3	annual
<i>Symplocos macrophylla</i>	5	5	1	1	2	2	?

^a Total number of trees of GBH > 10 cm

^b Fruit Availability Index (see methods)

^c Maturity judged as explained in methods

^d Fruit availability was determined for species with more than four mature trees. Pattern was considered annual at the population level if fruit were produced in both years (even by different trees) and supra-annual at the population level if fruit were produced in only one or neither year

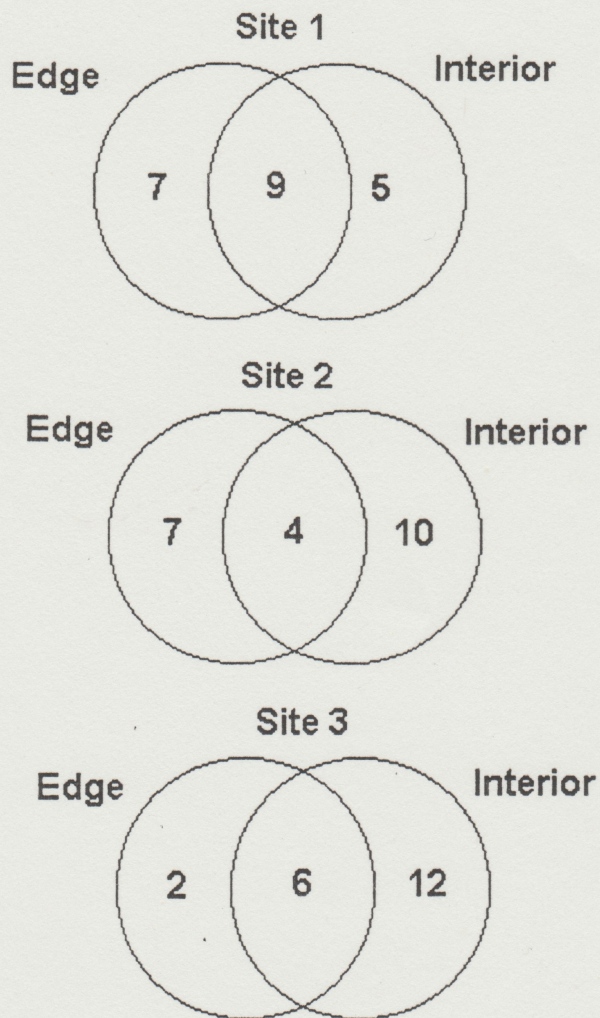


Fig. 4.1. Number of species found fruiting in edge and inner forest in year 1. Number of 78.5m² plots: site 1, edge = 12, interior = 12; site 2, edge = 6, interior = 12; site 3, edge = 6, interior = 12.

4.3.2.2 *Fruit abundance*

In both years there was no significant difference between site and zones in the density of fruiting trees or in the mean peak fruit score per mature tree. Species from all sites and zones were therefore pooled for further analysis.

In both years the distribution of mean peak fruit scores of mature trees was skewed (Fig. 4.2), with a median of 1.6 points in year one and 1.3 points in year two, out of a maximum potential of 4. Thus in both years most species produced less than 50% of their maximum potential canopy coverage of fruit.

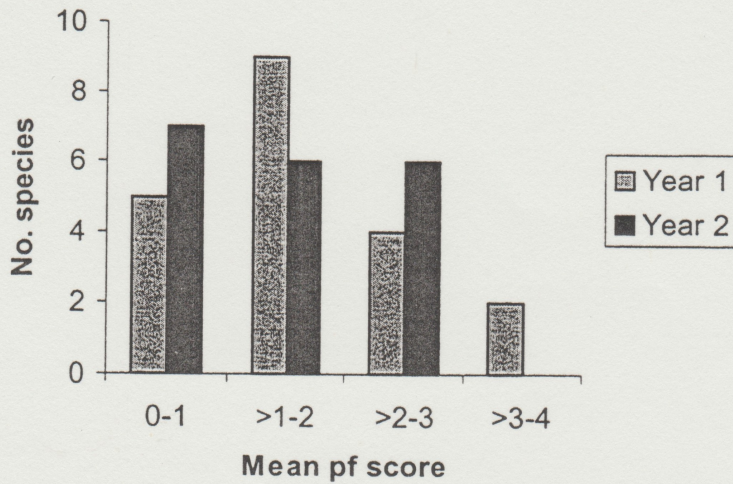


Fig. 4.2. Distribution of mean peak fruit scores of mature trees between species. Only species represented by at least four mature trees were included (n=19).

4.3.3 Comparison between potential and actual fruit production

Fruit was produced by $60.9 \pm 2.5\%$ of site-dominant species (Table 4.2, group 1.1c) per site, per year (mean and standard deviation of three sites and two years) (Table 4.4).

Of the 27 most common species (in three sites combined), 19 (70%) fruited in the first year and 18 (67%) fruited in the second year. Six species failed to fruit in either year (*Lithocarpus elegans*, *Phoebe lanceolata*, *Heliciopsis terminalis*, *Elaeocarpus floribundus*, *Artocarpus lanceolata* and *Rhus chinensis*) while five species only fruited in one year (*Castanopsis diversifolia*, *Beilschmiedia* sp. 1, *Phoebe* sp. 1, *Eugenia albiflora* and *Erythrina stricta*) (Table 4.3).

Table 4.4. Abundance and fruit production of site dominant species^a and others (grouped) at each site in each year, ranked by tree density.

Species	SITE 1					SITE 2					SITE 3				
	N ^b	Den ^c	FAI ^d		Species	N ^b	Den ^c	FAI ^d		Species	N ^b	Den ^c	FAI ^d		
			Yr1	Yr2				Yr1	Yr2				Yr1	Yr2	
<i>Castanopsis diversifolia</i>	31	164	8.0	0	<i>Styrax benzoides</i>	29	205	43.3	13.3	<i>Saurauia roxburghii</i>	10	71	38.0	31.8	
<i>Vernonia volkameriifolia</i>	22	117	75.6	66.3	<i>Castanopsis diversifolia</i>	17	120	5.3	0	<i>Eurya acuminata</i>	10	71	27.4	16.8	
<i>Helicia nilagirica</i>	15	80	22.5	9.9	<i>Castanopsis acuminatissima</i>	17	120	16.8	23.9	<i>Castanopsis tribuloides</i>	9	64	23.0	17.7	
<i>Wendlandia scabra</i>	12	64	0	18.6	<i>Schima wallichii</i>	10	71	14.1	8.8	<i>Vernonia volkameriifolia</i>	9	64	22.1	30.1	
<i>Engelhardtia spicata</i>	11	58	8.0	8.0	<i>Acronychia pedunculata</i>	9	64	49.5	35.4	<i>Castanopsis diversifolia</i>	8	57	0	0	
<i>Saurauia roxburghii</i>	10	53	35.8	37.1	<i>Lithocarpus elegans</i>	8	57	0	0	<i>Rhus chinensis</i>	5	35	0	0	
<i>Bellschmidia sp. 1</i>	9	48	15.9	0	<i>Litsea salicifolia</i>	8	57	3.5	7.1	<i>Lithocarpus elegans</i>	5	35	0	0	
<i>Glochidion acuminatum</i>	9	48	12.6	9.9	<i>Castanopsis tribuloides</i>	7	50	0	0.0	<i>Styrax benzoides</i>	5	35	24.8	4.4	
<i>Phoebe lanceolata</i>	6	32	0	0	<i>Eurya acuminata</i>	7	50	5.3	12.4	<i>Wendlandia scabra</i>	5	35	10.6	24.8	
<i>Helicopsis terminalis</i>	5	27	0	0	<i>Artocarpus lanceolata</i>	5	35	0	0	<i>Elaeocarpus floribundus</i>	4	28	0	0	
<i>Phoebe sp. 1</i>	5	27	0	0	<i>Phoebe lanceolata</i>	5	35	0	0	<i>Symplocos macrophylla</i>	4	28	7.1	5.3	
<i>Erythrina stricta</i>	5	27	5.3	0	<i>Sapium baccatum</i>	4	28	0	0	Other species (n=45)	65	460	63.7	62.7	
<i>Schima wallichii</i>	5	27	4.6	4.0	<i>Wendlandia scabra</i>	4	28	7.1	3.5						
Other species (n=28)	38	202	61.7	58.4	Other species (n=57)	76	538	71.6	86.7						
Total:	183	250	250	212	206	206	217	217	191	139	139	217	217	194	

^a Site dominant species are those with a density of at least 25 trees ha⁻¹

^b N = number of trees with GBH >10 cm at start of study

^c Den. = density of trees with GBH > 10 cm at start of study (number of trees ha⁻¹). Total area of plots at site 1 = 1884.96 m², site 2 and 3 = 1413.72 m²

^d FAI = fruit availability index as calculated in the methods.

4.3.4 Factors limiting fruit production

Supra-annual fruiting pattern

Four out of the 19 species examined had a supra-annual fruiting pattern (Table 4.3). *Castanopsis diversifolia* and *Beilschmiedia* sp. 1 both fruited in year 1 only, *Phoebe lanceolata* and *Heliciopsis terminalis* both failed to fruit in either year. The other 15 species fruited annually at the population level. *Heliciopsis terminalis* is a dioecious species, so some of the four trees in the sample may have been non-fruiting males. *Rhus chinensis* also failed to fruit during the study period but was not classed as supra-annual as it was observed fruiting annually elsewhere (see shade tolerance).

Shade intolerance

Shade intolerance accounted for failed fruiting of one out of the 27 most common species. *Rhus chinensis*, a monoecious species, was represented by 5 trees in year 1, of which 4 were seen to flower and were thus mature. Despite being seen to fruit prolifically each year in the clearings, no fruit was produced in the forest plots. It was concluded that this species was unable to fruit in the shade of the forest. This may also explain the behaviour of *Markhamia stipulata* and *Debregeasia longifolia* (represented by single trees in the forest plots) which also failed to fruit, while other similarly sized trees growing in clearings fruited prolifically. Such behaviour was not typical of all pioneer trees though; *Macaranga denticulata*, *M. kurzii* and *Glochidion acuminatum* did produce fruit in forest plots, albeit less than in the clearings.

Population structure

Seven of the 27 commonest species (26%) had a low density of absence of mature trees (i.e. less than 20% of trees ≥ 10 cm GBH). These accounted for four of the eight non-fruiting species in year 1 and four of the nine non-fruiting species in year 2.

Fruiting success of the 27 commonest species was related to density of mature trees. Fruiting species had a significantly higher density of mature trees than non-fruiting species in both years (Table 4.5)

Table 4.5. Density of mature trees: comparison of fruiting and non-fruiting trees

	Mean and standard error of density of mature trees (trees ha ⁻¹)		P ^a
	Fruiting species	Non-fruiting species	
Year 1	19 ± 4	5 ± 1	<0.01
Year 2	19 ± 4	6 ± 1	<0.05

^a Probability that the two groups are the same, according to a Kruskal-Wallis test

Common species with a low proportion of adult trees were: *Cinnamomum iners* and *Symplocos macrophylla* (fruited both years); *Phoebe* sp. 1 and *Castanopsis diversifolia* (fruited one year); *Lithocarpus elegans*, *Elaeocarpus floribundus* and *Artocarpus lanceolata* (did not fruit).

4.3.5 Relationship between species characteristics and fruit production

Despite inter-site differences in the species composition of the potential seed source, the distribution of species across seed type groups was very similar at the three sites (Fig. 4.3). A minority of species, 3 to 6%, had wind dispersed seeds. Of the non-wind dispersed species, all sites were dominated by species with medium sized seeds, 5.1 to 15 mm in length (43-55% of species), while the remaining species were equally divided between those with small seeds of up to 5 mm (16 to 25%) and large seeds of more than 15 mm (17 to 26%).

The seed type distribution of species in the actual seed source was different to that of the potential seed source (Fig. 4.3). Whereas the original pool of species was invariably dominated by species with medium sized seeds, at each site the distribution of all fruiting species showed an increase in the relative dominance of wind dispersed and small seeded species, and a decrease in the relative dominance of medium and large seeded species.

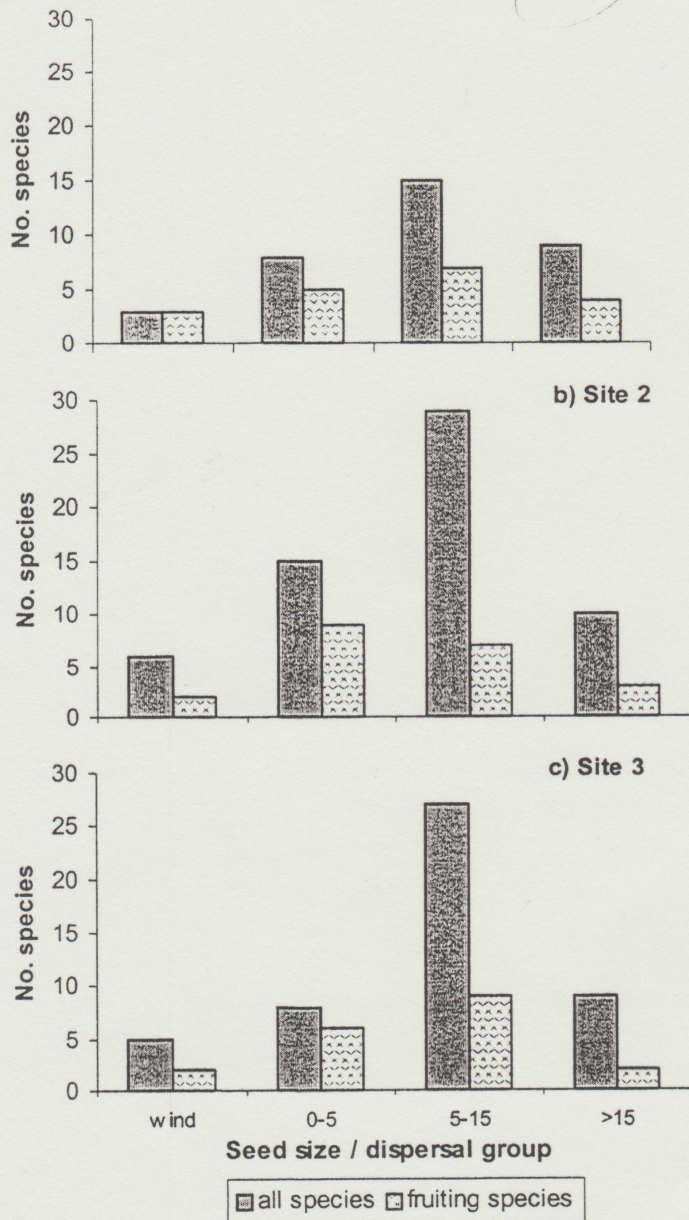


Fig. 4.3. Distribution of seed-type groups among all tree species in the plots and among the 47 species in the plots which bore fruit during the study.

Only species represented by trees with GBH \geq 10 cm GBH were included. Species are grouped by the following seed traits: Wind = wind dispersed seeds; 0-5 = seeds \leq 5 mm; 5-15 = seeds $>$ 5 mm and \leq 15 mm; $>$ 15 = seeds longer than 15 mm (Appendix I).

4.4 Discussion

The broad overlap between well-represented species confirms that, on a large scale, the three sites were representative of the same basic forest formation – that is, slightly degraded evergreen forest falling somewhere between Santisuk's lower montane rain forest and lower montane oak forest (Santisuk, 1988). On a smaller scale, inter-site differences in species' ranking may have been the result of elevation (site 1 was 200 - 300 m higher than sites 2

and 3), differing anthropogenic interference (chapter 2) or simply random clumping of individual species.

During the study period, the floristic composition of the fruiting species (the actual seed source) was broadly similar to the composition of the forest (the potential seed source). However, a key difference was that in each year of the study period, the actual seed source was less well represented by members of Fagaceae and Lauraceae, families, which had been an important component of the potential seed source. As the seed source is the starting point for forest regrowth in completely cleared areas, the limited availability of these dominant families means that the potential for regrowth of the forest in its original form is impeded from the beginning in some years. The results for *Beilschmiedia* sp. 1, *Phoebe lanceolata* and *Castanopsis diversifolia*, supported by local knowledge and personal observations, indicate that synchronised supra-annual fruiting is common in these families. So although fruit was limited during the study period, it may be abundantly available in some years.

As species of Fagaceae and Lauraceae tend to have medium and large sized seeds, the limited fruiting of these dominant families partly explains the relative shortage of medium and large seeded fruiting species. Other common, medium to large seeded species, which failed to fruit during the study period, included *Heliciopsis terminalis*, *Artocarpus lanceolata* and *Elaeocarpus floribundus*.

The skewed distribution of mean peak fruit scores among species (Fig. 4.2) occurs because few mature trees achieve full fruiting potential. This finding is in agreement with Bullock and Solis-Magallanes (1990), who found abundant fruiting to be very uncommon in Mexican deciduous forest.

The results indicated that species with a low density of adult trees were less likely to bear fruit in a given year than common species. This could be due to poor pollination due to the wide spacing of trees, as has been shown for *Shorea siamensis* (Ghazoul *et al.*, 1998). An alternative explanation is sampling error. If a species is represented by a very low density of adults and there is non-synchrony of fruiting among trees, then fruit availability in a given area may be effectively supra-annual, simply because the few trees in that area happen to be all in a non-fruiting phase. For example, *Lithocarpus elegans* failed to fruit in the plots even though a fruiting tree was observed outside the plots. Whatever the explanation for the results, there is no doubt that rarity of mature trees is a factor limiting fruit availability for regeneration. Assuming that trees in the forest around a cleared area provide the seed source for regeneration, then the level of fruit production in the population as a whole is irrelevant if fruit production is limited by the small "sample" of trees in the local area.

Anthropogenic interference is one factor that may lower the density of mature trees. In site 2, next to the village, 16% of trees in the inner forest plots were lost due to cutting or ringbarking during the study in contrast to site 3, further from the village, where only 2% of trees were lost in this way. It was anticipated that the human activity at site 2 may have

reduced the density of mature trees and thus limited fruit availability. However, it appears that most of the cutting was of small immature trees and although a few large mature trees were also removed, any effect on fruit availability was undetectable in a study of this scale. Both the number of fruiting species and the level of fruit availability were similar at the two sites, which were otherwise comparable in terms of elevation and number of plots.

The results showed no significant difference in fruit production between the forest edge and inner forest. It is possible that the zone effect was not significant due to the high inter-plot variability within zones. At sites 1 and 3, the forest canopy was discontinuous in places due to fire damage, so it is likely that light levels in the inner forest were not significantly lower than at the clearing edge, thus accounting for the similar levels of fruit production. At site 2, the clearing was rectangular, lying along a shallow valley oriented north-south. As a result, the long forest edges, where the edge plots were located, were in shade for much of the day, which may also have created a similar light environments to the inner forest.

The significance of infrequent fruit production as a limiting factor depends on the length of opportunity for tree establishment from seed in clearings. If this period is short, as suggested in chapter 3 and by Finegan (1996), then the findings of this study are highly significant, as supra-annually fruiting species may miss their opportunity to colonise the clearing if the timing of clearance does not coincide with masting. If the period is long, or indefinite, supra-annual species would only be at a relative disadvantage compared to annual species, there being fewer years in which seed was available for colonisation. Species with a low density of mature trees would be limited irrespective of the above.

4.5 Conclusion

- Around one third of common species failed to produce fruit each year.
- Fruit production did not vary between sites or forest zones despite differences in human intervention between the three sites.
- Around one fifth of species tested failed to fruit in at least one year due to a supra-annual fruiting pattern.
- Species with a low proportion of mature adults (around one quarter of those tested) had a lower probability of producing fruit.
- Intolerance of forest shade was not an important limiting factor and may have prevented fruiting in one (possibly three) species tested.
- The medium to large seeded species, which were dominant in the forest canopy, fruited less frequently than smaller seeded species and so their seed availability was temporally more limited.