PHENOLOGY OF SELECTED TROPICAL TREES FROM JARI, LOWER AMAZON, BRAZIL

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ABSTRACT

The phenology of flowering, fruiting and vegetative states of trees were surveyed through 36 consecutive monthly observations of 1508 trees of 137 species of 15 families from the Jari river basin, lower Amazon, Brazil. The communities studied comprised eight distinct forest sites that included seven upland and one seasonally flooded forest site, located within one degree of latitude and longitude. In order to investigate the effect of soil on tree phenology a survey was carried out on the soils occurring under the eight forest sites studied. Phenological results obtained were analysed at individual, population and community levels. Results are firstly presented at species (population) level arranged by plant family. Then community phenology is considered by summing the phenological events of all individuals in each particular forest. The forests of Jari showed very clear seasonal patterns of leaf shedding as well as of flowering and fruiting. No significant distinction was found between flowering and fruiting phenologies between the eight forests studied within a particular time. The influence of the environmental factors upon phenology is evaluated by comparing the median fruiting phenologies of different populations of the same species which differ (if at all) only in location parameter. Environmental variables tested in Chapter 6 did not affect tree phenology on a community basis. However, tree phenology of the Jari micro-region was strongly correlated with rainfall. To investigate the
influence of the genetic (internal) factors to phenology. The synchrony in flowering and fruiteding time was calculated for 10 species of very restricted distribution. No perfect synchrony was found, neither between an individual and its conspecifics nor between all individuals of a population. Only some 20 per cent of the Jari trees flowered even at the peak of flowering activity. Six general models are proposed to describe the most common patterns of flowering and fruiteding phenology encountered, subdivided into cyclic (or seasonal) and acyclic (or aseasonal). The fruiteding phenology of congeners is also analysed at both sympatric and allopatric levels. Although some species had significantly different fruiteding dates from their congeners, most species tended to have overlapping fruiteding irrespective of being either sympatric or allopatric.
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To all the above people and institutions my most profound gratitude.
CHAPTER 1. INTRODUCTION

1.1 WHAT IS PHENOLOGY?

Phenology is the study of seasonal timing of life cycle events (Rathcke & Lacey 1985). A more elaborate definition is 'the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species' (Lieth 1974).

Observational studies developed in the last two decades have shown that patterns in flowering and fruiting times do occur in all ecosystems to a greater or lesser extent. Even tropical rain forests which do not experience major climatic changes throughout the year have a season when the rainfall is less pronounced. This, together with minor changes in photoperiod, are enough to cause variations in the reproductive and vegetative phases of trees. It has been hypothesized that the seasonal climatic variations of both tropical and temperate regions influence fluctuations in pollinators, frugivore-dispersers, predators and competitors (Lieberman 1982).

The present work is based on the following assumptions: (i) that flowering and fruiting phenology of tree species were shaped by natural selection; (ii) that pollinator and disperser availability are resources to which the trees either compete for or develop adaptations to avoid such
competition. The hypothesis to test this assumption considers the character displacement of the phenological behaviour. The full methodology utilized in the present investigation is provided in Chapter 3.

1.2. IDENTIFICATION OF THE PROBLEM

The importance to biology of the study of the development of flowers and fruits is due to the fact that these structures are related to the biotic and abiotic environment. The flowering patterns in plants are linked not only to the timing, duration and frequency of flowering but also to the form of reproduction of each species. It has been demonstrated that most tropical trees are not only outcrossers but also animal pollinated (Kalin-Arroyo 1979, Bawa 1974, 1983, Sobrevila & Kalin-Arroyo 1982) and that the tropical forest is characterized by having a low proportion of wind pollinated plants (Janzen 1975). As outcrossers the tropical trees need pollinator vectors to reproduce. For this reason interspecific competition for pollinators, pollinator availability and nature of flower rewards have been considered as the most critical factors controlling flowering (Bawa 1983).

Despite the increasing interest in tropical ecology, we still know very little about the phenology of tropical and subtropical tree species (Stern & Roche 1974, Frankie 1975, Augspurger 1983).
A critical review of the phenological literature appears later in Chapter 4. This shows the various advances accomplished in tropical tree phenology in both the Old and the New World. Many of the areas previously investigated are dealt with in this thesis in more detail. New topics are investigated and novel approaches suggested.

One aspect of tropical phenology much neglected concerns the detection of patterns in particular taxonomic groups. For example, in the neo-tropics only two phenological studies were carried out at family level, one by Gentry (1974) and the other by Mori & Prance (1987a). However, only Mori & Prance’s study concerns a family of tropical trees. Later in Chapter 5 the phenology of 15 plant families will be investigated with observations of 137 tree species.

A second area concerns the comparative study of different communities within a single microregion. This thesis includes data on 1508 trees found in eight distinct forest sites. These forests are separated by less than one degree of latitude and longitude. The physical aspects of the study area are presented Chapter 2. In Chapter 6 phenological results are presented both at the community level and for the entire region of Jari, while Chapter 7 investigates the influence of the environment and that of genetics upon tropical tree phenology.
It is the object of modern biological science not only to study the past but also to make predictions about the future. For each of 36 months, data on the flowering and fruiting of 137 tree species allows one to visualize the patterns that these phenomena exhibit. In Chapter 8 these patterns are discussed by means of graphical models.

Many of the common families of tree species found in the Amazon have genera with a large number of species that are very similar to one another. Some still have very small and inconspicuous flowers which are likely to attract the same pollinators. Knowing that the majority of the tropical rain forest trees are outcrossers and animal pollinated, it follows that pollinators are resources that the similar tree species would compete for if they become limited. In relation to fruiting, there is evidence that the embryos and seedlings of trees have a greater chance to survive and establish when they are carried away from the parent tree by frugivore-dispersers than if left underneath the parent tree. As a result, dispersers are another resource that tropical trees would compete for. If Gause’s exclusion principle (Gause 1934) were true then the similar species occurring in the same area (sympatric congeners) would do so by avoiding competition for pollinators and dispersers. Evidence for this hypothesis would exist if the difference in the phenological pattern is indeed higher between competing species occurring in the same area than between noncompeting species occurring in different areas.
The results of the soil study carried out in the eight forest sites studied is given in Chapter 10. An appreciation of the effect of soil in tree phenology is also provided there.

1.3. OBJECTIVE AND METHODS OF THE STUDY

The objective of this investigation is to describe the phenological responses of a selected number of Amazon tree species in relation to internal and environmental forces. This will be accomplished by two approaches. The first is the observational-comparative method, which concerns the analysis of the data at individual, population, species and community levels. These results will be presented in Chapters 5 through 8. The second approach concerns the use of the hypothetico-deductive method by which the phenological data are used to test Gause's principle of competitive exclusion by way of a hypothesis that the phenological character displacement among similar species is larger when such species are sympatric than when they are allopatric. The alternative hypothesis is that correlations between potential selective pressures and the process of evolution are unpredictable by phenology alone. This result will form the core of the material presented in Chapter 9.
1.4. RELEVANCE OF THE STUDY

The study of the development of flowers and fruits including their phenology is a major part of systematics and evolutionary biology. These structures are not only used for identification and classification but are also primary means of adaptation which provide clues about the earlier groups of plants that existed on the planet (Ashton 1988). Since most trees of the tropical forests are outcrossers (Bawa 1974, 1983, Kalin-Arroyo 1979, Sobrevilla & Kalin-Arroyo 1982), the significance of flowering and fruiting phenology is due to the interactions of flowers and fruits with pollinators and dispersers. However, few phenological studies have been carried out in tropical forests, particularly in the Amazon, compared with other areas of the world. Although there has been an increase in the number of publications dealing with the subject of tropical phenology only a few have presented empirical results and fewer even have analysed such results in the light of scientific evidence.

In general terms a worldwide view of seasonal patterns in forest phenology is needed for a complete understanding of forest genetic systems and ecosystems. The importance of such phenological patterns for ecosystems is due to the effect of the quality and abundance of food for forest animals. The study of various primary forest communities within one microgeographic region may permit the evaluation of the extent of microgeographic variation in abundance of
flower and fruit. In specific terms phenology can be useful in the study of animal-plant interactions related to pollination, dispersal and seed predation (Frankie et al. 1974a,b).

Since 1960, the world's rain forests have been subject to continuous threats not only of the accelerated demands for hardwoods but also by the encroachment of new settlements, agriculture and industry. Ecosystem research is needed to answer pertinent questions related to the management of natural resources. However the lack of experimentally derived information and systematic observations on Amazon ecology limits the precise assessment of the likely impact of development projects.

Tropical phenological studies are also important for genetic resources conservation since the vital statistics of trees are necessary for the management of tropical forest reserves, especially those aimed at 'in situ' conservation of genetic resources. Also, the detected variability in flowering and fruiting time and its duration can be very useful for tree breeding research and silviculture since it is an indication of the genetical discontinuities among individuals and populations.

1.5. PROBLEMS OF TROPICAL FOREST TREE PHENOLOGY

Although tropical tree phenology is considered essential to the development of tropical ecology and conservation (Croat
1969, Kemp et al. 1976) this type of study can be difficult and lengthy. It has been pointed out that a phenological study demands long term observations of many individuals of each species (Ducke & Black 1954, Stern & Roche 1974, Croat 1969). Secondly it has been pointed out that the phenological studies must be carried out on intact ecosystems, rather than on disturbed ones (Frankie et al. 1974b, Howe 1984). Thirdly it has been pointed out that proper phenology should include different habitats (Salisbury 1921, Ducke & Black 1954, Howe 1984). The biggest problem is finding enough individuals of the less common species since the Amazon forest has typically a large number of tree species represented by widely dispersed individuals. Another problem is access to various types of undisturbed forest habitats, since most forests which have road access also have human disturbance. For the reasons above there are few ecological studies carried out on primary 'terra firme' forests and those few that have been carried out focused on a small number of the commonest tree species.

The lack of appropriate quantitative techniques is a further major problem in the study of phenology (Gleeson 1981). It follows from the preceding paragraph that many tropical ecology experiments have small sample sizes (this one included), requiring careful statistical analysis principally by non-parametric methods. Many phenological studies in the tropics have been limited to the description of phases through time, and the results interpreted loosely
in the light of descriptive environmental features, both abiotic and biotic. Attempts to interpret tropical data in the light of temperate derived ecological theory have failed in many cases. One of the best examples, dealt with in Chapter 9, is the use of speciation theory to explain the habitat sharing of the closely related species in the tropical rain forest.

Ribeiro and Castro (1986) have proposed a quantitative method to evaluate phenological characteristics of trees. Their method involved the angular transformations of the frequencies obtained by classifying the percentages in fixed intervals. This method, which may be very adequate for forest plantations, has some limitations to be used in tropical rain forest phenology. Firstly the transformed data could lose its ecological significance. Secondly, original percentages obtained from a small sample size may lead to uncharacteristic results. Finally it is only adequate for trees that are not too tall and with well studied biology.
CHAPTER 2. THE STUDY AREA

2.1. LOCATION OF THE AREA

The field work was carried out in the area between the rivers Paru and Jari, in the lower Amazon. These rivers are the two major easternmost tributaries on the northern bank of the Amazon river before it reaches the Atlantic ocean (Fig. 2.1). The area studied includes the town of Monte Dourado (County of Almeirim, Pará) and a large area of the County of Mazagão (Amapá). These two county names are important to mention for the botanical history of the area, as both are mentioned in Spix and Martius' diary of their travels to the Amazon and Rio Negro from 1819-20 (Spix & Martius 1938). Geographically the studied sites are close to the Equator, ranging from 0027' to 106' Latitude South and 52051' to 52025' Longitude West.

The economic importance of the area is based on the forestry activities of the Jari Company, former 'Jari Project'. The forestry and industrial operations are carried out by its subsidiary, Companhia Florestal Monte Dourado. This last has large forestry plantations, and a pulp mill producing 250 tons of cellulose per month. The forest crops are of three species: Gmelina arborea Roxb., Pinus caribaea Morelet var. hondurensis Barr. & Golf. and Eucalyptus spp. In addition to these three, several other tree species have been introduced experimentally. Other economic activities of the Jari Company include
exploitation of kaolin and bauxite by parallel companies or subsidiaries. The company was founded in 1967 by the North-American entrepreneur Daniel Keith Ludwig, who later sold it at a great loss to the Brazilian consortium, in 1982 (Coutinho in prep.).

2.2. LOCATION OF THE SITES.

The phenological study was carried out in eight sites of primary forest within reserves (Fig. 2.1). All but one site belong to the Jari Company. However, they are all part of a complex of genetic reserves (The Jari Genetic Reserve), aimed to promote 'in situ' conservation of forest genetic resources, which the Company implemented through a cooperative agreement with CENARGEN (The Brazilian National Genetic Resources Centre) from 1985 to 1987. The eighth site belongs to the Federal Government, and is part of the Jari Ecological Station, administered by IBAMA (Brazilian Environmental Institute).

Table 2.1 shows the locations of each forest studied as well as a summary of other relevant information. Details about environmental factors of the area will be given separately.
Table 2.1. Geographical gradient of the forest sites studied at Jari, Brazil.

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Coordinates</th>
<th>Altitude (m)</th>
<th>Size (ha)</th>
<th>Forest Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angelim</td>
<td>01006'S 52925'W</td>
<td>77</td>
<td>400</td>
<td>Savanna</td>
</tr>
<tr>
<td>Quaruba</td>
<td>01002'S 52920'W</td>
<td>141</td>
<td>987</td>
<td>Savanna</td>
</tr>
<tr>
<td>Mt. Dourado</td>
<td>01001'S 52923'W</td>
<td>76</td>
<td>150</td>
<td>Semi-open</td>
</tr>
<tr>
<td>Mt. Felipe</td>
<td>00252'S 52923'W</td>
<td>150</td>
<td>306</td>
<td>Semi-open</td>
</tr>
<tr>
<td>S. Militao</td>
<td>00246'S 52940'W</td>
<td>113</td>
<td>1,973</td>
<td>Semi-open</td>
</tr>
<tr>
<td>Pacanari</td>
<td>00239'S 52935'W</td>
<td>107</td>
<td>750</td>
<td>Semi-open</td>
</tr>
<tr>
<td>Itapeuara</td>
<td>00235'S 52939'W</td>
<td>37</td>
<td>300</td>
<td>'Várzea'</td>
</tr>
<tr>
<td>IBAMA</td>
<td>00227'S 52951'W</td>
<td>449</td>
<td>500</td>
<td>Dense</td>
</tr>
</tbody>
</table>

Figure 2.1. Map of the Jari-Parú basin showing the location of the eight forests studied.
2.3. CLIMATE AND WATER RELATIONS

The area of Jari has a climate formula B1rA'a' on the Thornthwaite system, or 'Amw' on the Köppen system. The climate is hot and humid, with average temperatures in the order of 26.4°C. The average yearly precipitation is 2,115 mm. This high precipitation average compensates for a mild dry season which takes place from August to December. The driest months, September to November, contribute with only 8% of the annual volume of rain in the region (Correa et al. 1989). The Jari Company maintains six thermopluvimetric stations throughout its area. The information in Figure 2.2. was taken from these stations during the period when the phenological observations took place.

![Figure 2.2. Rainfall (*) and temperature (-o) of Jari.](image)
2.4. GEOLOGY, GEOMORPHOLOGY AND RELIEF

The Jari river is located within the Amazon Basin and thus shares the same geological history. Several overviews are now available on the geology of the Amazon, such as that of Fittkau (1974), Schubart (1983), Putzer (1984), Radambrasil (1972-78) and Daly and Prance (1989). Therefore in this section I will only describe the geological features which are characteristic of the Jari area.

The Jari region is located in between the Purus and Gurupa arches or areas of orogenic uplift formed on the underlying crystalline rocks of the Precambrian shield formed some 3,500 million years ago (Putzer 1984).

On the north of the studied area, somewhat in the midcourse of the Jari-Parú rivers there are outcrops of Paleozoic sandstone and siltstone sediments forming a sequence known as the Trombetas-Maecuru Formation (Figure 2.3). They occur over a 450-600 m plateau (Figure 2.4) with altitude corresponding to the level of the Plio-Pleistocene Pediplane (Pd2), which was preserved by the presence of an existing iron duricrust (Pires in press). These Paleozoic sediments overlay the even older crystalline rocks of the Uatumã Series, which occur as twin bands on both sides of the Amazon river. The northern strip extends between the rivers Negro and Jari. The Uatumã Series is thought to have resulted from a series of volcanisms that pierced the
Guiana craton still extending to that area (Putzer 1984). The resulting volcanic rocks of the Uatumã Series are cut by the northern tributaries of the lower Amazon such as the Parú and Jari rivers themselves leading to the present waterfalls and rapids. The remarkable feature of the Jari landscape is the long scarp, over 50 Km, which was formed in the direction E-NW along the outcropped Paleozoic sandstone (Figures 2.3 and 2.4.)

As in the rest of the Amazon basin most of the sediments found in the area of Jari are of Tertiary origin being part of the Barreiras Formation. Spread among the Tertiary terrains (Barreiras Formation) of Jari there are two types of terraces or table-top hills which are considered part of the Belterra Formation (between the Tertiary and Quaternary) (Figure 2.4). The first type of terrace, with altitude between 135 and 200 m (Pd1) was made by eroded Pliocene and Pleistocene surfaces. The second type, made by irregular and dissected hills of altitude between 68 and 74 m (P2), were made by sediments of the former (Klammer 1971, 1978). The soils of the Barreiras Formation are unconsolidated and made of ferruginous sands (Radambrasil 1972-78) while the soils of the Belterra Formation are more compact and formed by kaolinitic clays (Klammer 1971).

The presence of these two geological formations creates a less homogeneous landscape than that found in most parts of the Amazon basin giving a variety of soil types and consequently a less homogeneous vegetation.
Quaternary deposits occur only on the margins of both the Amazon and the Jari and Paru rivers.

The relief types found in the area of Jari permits the separation of the various geological formations and consequently the soil types found there. For this reason the altitude of the eight sites studied as well as that of some other important reference points was measured by recording a series of measurements taken by two portable altimeters (Table 2.1).
Figure 2.3. Diagram showing the geomorphology of the Jari-Parú landscape.
Figure 2.4. Diagram showing the relief of the Jari-Parú landscape.
2.5. SOILS

2.5.1. Amazon Soils

The luxuriance of the Amazon forest gave rise to the myth of the extreme fertility of its soils. This misconception started with the account of the Jesuit Father Cristobal Acuña who narrated the Teixeira Amazon expedition of 1639 (Sioli 1984). Even scientists such as Alexander von Humboldt and Aimée Bonpland, after their epic voyage through the Amazon and Orinoco basins from 1799 to 1804, wrote that such luxurious vegetation could only grow on a highly fertile soil (Humboldt and Bonpland 1819). In fact, the soils of the Amazon basin are among the poorest in chemical elements on earth (Sombroek 1984, Camargo 1981, Herrera et al. 1978).

To explain the paradox of the luxurious forest on such poor soils, ecologists have come up with several models of nutrient closed systems. One of the most accepted of such models suggests that in the Amazon the soil nutrients are kept mainly on the litter layer and are extracted by the root-mat arranged in the first 20 - 40 cm of the top soil, forming a tight system that minimizes nutrient loss. The density of such root mat is three times that of temperate zone soils (Klinge 1973), and its depth is inversely proportional to the nutritional status of the soil.
The poverty of the Amazon soils has been attributed to the severe leaching resulting from the rapid decomposition of litter caused by the frequent heavy rains that occur in the area. But not all Amazon soils are poor and several ecologists such as Jordan and Herrera (1981) and Lathwell and Grove (1986), among others, have called attention to the variation that can occur among them. It is possible to generalize that the extreme poverty in mineral nutrients found in most Amazon soils can be attributed to the fact that they were made mostly from weathered granite rocks and because they were heavily leached before they were deposited. Only six per cent of Amazonia has well drained fertile soils (Cochrane 1984).

The nutrient budget of the Amazon basin soils under natural vegetation are thought to be correlated with the nutrient budget of its drainage waters (Fürch & Klinge in Herrera et al. 1978, Sioli 1984). Thus the richer soils would occur in areas of white water rivers and the poorest on areas drained by blackwater rivers, such as the Rio Negro, while soils from areas drained by clearwater rivers are also very poor in nutrients. The vegetation patterns found in the Amazon are also thought to be correlated with its various secondary hydrographic basins (Pires & Prance 1985, Simpson and Haffer 1978). Except for nitrogen, the bulk of the elements (nutrients) in the soil is related to the types of rocks which form its substratum (Jenny 1980). The majority of the nutrient stock of the Amazon soils are concentrated in the first 10-15 cm of top soil (Wambeke 1978).
In contrast with the soils of the permanently dry areas, the soils of the alluvial floodplains or seasonal ‘várzeas’ are highly fertile. This is due to the deposition of nutrient-rich silt during the periodical inundations that occur in such areas. But not all Amazonian floodplains have the same soil fertility. The ‘várzeas’ on the margins of white-water rivers are the most fertile ones whereas those of the black and clear-water rivers are the least rich.

The first extensive study of the soils of eastern Amazon was carried out by a FAO consultant, Soembroek, in 1966. After that much progress was accomplished during the seventies by the RADAM project, later RADAMBRASIL, which made small-scale inventories of the Amazon’s natural resources by the use of radar images (RADAMBRASIL 1972-78). Researchers of the Brazilian National Soil Survey and Conservation Service (EMBRAPA/SNLCS) utilized the radar images published by the RADAMBRASIL Project to make the most updated soil map of Brazil, in a 1 : 5,000,000 scale (Camargo 1981).

2.5.2. Soils of the Jari basin

The first observations about the soils of Jari were recorded in a report made by Falesi, in 1969. A soil laboratory and a network of meteorological stations were installed in the mid-seventies by the Jari Company, to study the soils of the areas where plantation forestry
would replace natural forests. The nutrient balance of areas of cultivated forest in Jari was studied in detail by Russell (1983). That study compared the nutrients of various areas of plantation forestry with soils occurring under one site of natural forest. A large-scale soil survey of the Jari-Paru area was completed in 1987 by researchers of the Jari Company and EMBRAPA/SNLCS (Correa et al. 1989), covering only soils of the plantation areas. The present study covered the soils under natural vegetation. Samples for the physical and chemical analysis were taken from selected pits dug in the eight forests where the phenological observations took place. Results of this study together with an appreciation of the influence of soils upon phenology are provided in Chapter 10.

Relief and climate have been and are the essential factors controlling rates of decomposition, transport and sedimentation (Putzer 1984), which influence the landscape. The Jari-Parú landscape is a result of complex interactions between its geomorphology, rivers and climate. The four major features of the Jari landscape are described in 2.4. The soils of the Jari basin are related to the overall landscape of the area, which in turn is much influenced by the area’s geology as well as by certain aspects of the Jari and Paru rivers. These rivers cut through the ancient uplands of the Guyana Shield bringing sediments which are mixed with those carried by the Amazon river. The fact that the Jari and Paru rivers are intermediate from black to
clearwater rivers indicate that the soils of these basins are among the poorest in the Amazon.

The eight forest sites studied cover every subdivision of the Jari basin landscape. They include a seasonally flooded forest or 'várzea' (Itapeuara), two forests on 68-74 m alluvial valleys (Angelim and Quaruba), one in a 145-200 m terrace (Felipe), three on intermediate hills (Monte Dourado, São Militão and Pacanari) and one on the 450 m planation surface (IBAMA – Jari Ecological Station) (Figures 2.1, 2.3 and 2.4). Since the climate of the Jari basin is homogeneous, edaphic factors can be looked upon to explain the differences in species composition and richness found in the various forest sites studied (Pires in prep).

2.6. THE NATURAL FORESTS OF JARI

Although vegetational patterns found in the Amazon are thought to correlate with the geography of its hydrographic basins (Pires 1984, Pires & Prance 1985), the inventories carried out at the various forests of Jari showed an appreciable degree of variation. Since the studied sites fall within only one latitudinal degree we can assume that rainfall and temperature are constant and soil can be the most likely factor to account for the variation encountered.
The major vegetation of Jari is the semi-evergreen equatorial forest, simply referred to as tropical rain forest. The term semi-evergreen is used because most of the trees exhibit a great deal of leaf loss during the dry season (August to December), when the trees’ canopies are reduced by up to 30 percent.

Botanical and ecological studies carried out in the eight forest reserves of the Jari Company (Pires in prep.) revealed that such forests differed significantly in tree species composition and in forest height. They also differed by the occurrence of a babassu-related stemless palm, *Orbignya sagotii* Trail ex Im Thurm (M.J.Pires & N.T.Silva-1626), known as palha-pretta. This palm species can be used as an ecological marker in the same fashion as the babassu palm (*Orbignya phalerata* Mart.) is used to distinguish the transition forests found in the State of Maranhão from the typical Amazon forest. In the area of Jari this palm occurs in high numbers on the poorest sandy soils, in average numbers on the clay soils, being completely absent in the loamy soils under the forests which occur in the high planation surfaces of NW Jari. In Jari only the latter can be considered typical dense forests, the remaining ones being all semi-open, from mesic to dry.

The original vegetation of Jari is a continuous semi-open forest with Brazil-nut trees (*Bertholletia excelsa* H. & B.). Its distinct types as well as intermediate forms are
seen today in the present reserves which are maintained by ‘Companhia Florestal Monte Dourado’. A small percentage of high and low savannas also occur in association with rock (clastic) substrates (Pires in press). From the air it is possible to detect the different canopy heights of the Jari forests. The lowest ones occur on well drained ultisols and alfisols, where water is less available to plants during the dry season, in spite of the same annual precipitation of the areas considered. In some areas the canopies are higher due to the influence of larger water courses and more clayish soils. At the 500m plateau where the Jari Ecological Station (Ibama) is located the forest canopy is the highest. The major forest types that occur in Jari are:

1. Semi-open dry forests with *Orbignya sagotii*. Occur in low undulating plains, over Tertiary base of the Pliocene Barreiras Formation, mainly in sandy facies. Soil profiles on these areas observed in roadside cuts show stone lines. In these forests the canopy does not reach more than 25 meters, although in some areas there are extensive associations of emergent species such as *Dinizia excelsa* Ducke and *Qualea paraensis* Ducke. These dry forests or ‘campinarana’ or ‘Amazon caatinga’ forests have a much smaller number of tree species with a larger population density than found elsewhere. Sunlight reaches about 30 per cent of the soil on cloudless days, resulting in a relatively dense undercover which includes many grasses and sedges. The major tree species in decreasing order of frequency are: *Saccoglottis guianensis* Benth., *Vochysia*
obscura Warm., Licaria heteromorpha Benth., Humiria balsamifera (Aubl.) J.St.Hil., Protium sagotianum Marchand, Dinizia excelsa Ducke, Sclerolobium melanocarpum Ducke and Qualea paraensis Ducke. The first two show some domination in certain areas. The ten most frequent species make up more than 50 per cent of all the trees found in those forests.

2. Semi-open mesophytic forests with Orbignya sagotii. This formation also occurs in the lowplains over Tertiary base sediments, in sandy to loamy-sandy facies. The forest canopy varies from 25 to 40 meters. Here the amount of sunlight that reaches the forest floor is smaller than in the previous forest described. No grasses or sedges are found, except in the disturbed borders. The major tree species in decreasing order of frequency are: Geissospernum sericeum Benth. & Hook., Laetia procera (Poepp.) Eich., Mouriri callocarpa Ducke, Persea jariensis Vattimo-Gil, Micropholis venulosa (M.E.) Pierre, Protium giganteum Engl. and Vouacapoua americana Aubl. In certain areas there can be some dominance of Geissospernum sericeum Benth. & Hook. and Laetia procera (Poepp.) Eich., which are heliophytes associated with the gaps formed by frequent tree fall in areas where the soil is very stony. The Brazil-nut trees (Bertholletia excelsa) occur scattered, as emergents, in these forests.

3. Semi-open mesophytic forest with Orbignya sagotii over plateaux. This type of forest occurs on the 150 - 200 m
table-topped hills or terraces which are common in the lower Amazon, of Plio-Pleistocene origin (Klammer 1971, 1978). The soils on these terraces have medium to heavy clay texture. The forest canopy reaches 40 m, and the understorey vegetation is dense, with many small palms, due to the amount of light that reaches the ground. This forest characterizes itself by the low number of leguminous species and the high number of Sapotaceae. Another feature is a high percentage of trees with diameters less than 10 cm, especially on the edge of the slopes. This may be due to a possible past seral stage, when competition for light was higher. The major tree species in decreasing order of frequency are: *Thyrsodium guianense* Sagot, *Manilkara amazonica* (Hub.)Standl., *Micropholis guianensis* (A.DC.)Pierre, *Protium sagotianum* Marchand, *Virola michelii* Heckel, *Hirtella piresii* Prance, *Pouteria anomala* (Pires)Penn. and *Syzygiopsis oppositifolia* Ducke. This forest has few heliophytes and the first three species may show some degree of dominance.

4. Closed dense forest without *Orbignya sagotii*. These forests occur over the highest planation surfaces of the lower Amazon, at 440 - 500 m, over Paleozoic sediments. Soils are mostly of well textured sandy-clay-loams with high amount of iron oxides and other nutrients. The canopy can be higher than 40 m, while some emergents such as *Huberodendron swietenioides* (Gleason) Ducke, *Cedrelinga cateniformis* (Ducke) Ducke and *Dinizia excelsa* Ducke may reach 50 - 60 m. The ground cover is dense only during the
rainy season, when the tree trunks are entirely covered by mosses and epiphytic ferns. Palm trees occur in the over and understoreys, but in smaller amounts than in the other forests. This forest is characterized by the absence of the palm Orbignya sagotii (palha-preta) as well as of chrysobalanaceous species (both associated with poor soils) as well as by having several tree species which do not occur elsewhere such as Huberodendron swietenioides and Cordia goeldiana. Other features of this type of forest are the lack of dominance of any tree species and the very high tree diversity. The twenty most common tree species make slightly less than 40 per cent of the total. Over twice as many tree species were found here than in the dry forests described. The major tree species in order of population density are: Carapa guianensis Aubl., Qualea rosea Aubl., Guarea kunthiana A. Juss., Inga thibaudiana DC., Protium pallidum Cuatr., Eschweilera pedicellata (Richard) Morí, Virola michelii Heckel, Thrysodium spruceanum Benth., Pourroma vilosa Trec., Vouacapoua americana Aubl. and Persea jariensis Vattimo-Gil.

5. Seasonally-flooded forests with lianas ('várzea' forests). These forests occur on both sides of the Jari river, over gleys. Although its major characteristic is the annual floods, some areas of it are slightly elevated and may remain dry throughout the year. A high amount of woody lianas occur in these forests. The most frequently occurring tree species are: Pentaclethra macroloba (Willd.)Kuntze, Duguetia sp., Marmaroxylon racemosum
(Ducke) Killip, Pouroma villosa Trec. and Hevea brasiliensis Muell.Arg. The first two species make up about 20 per cent of the total number of trees. The ten most frequently occurring trees make up 43.3 percent of the total.

Although a vegetational uniformity is expected within a hydrographic basin many variations still occur due to variation of the soil. However, the differences in forest types found in the Jari basin are expected to be smaller than the differences found between these forests and those belonging to other hydrographic basins of the Amazon.
3.1. SELECTION OF THE SPECIES STUDIED

The tree species included in this study were identified during botanical surveys carried out between 1985 and 1987 in eight genetic reserves. These surveys were part of a project of 'in situ' conservation of genetic resources coordinated by the Brazilian Genetic Resources Centre (CENARGEN) through a cooperative agreement with the Jari Company. As a result of such surveys some 9,000 retrievable trees were recorded in the eight forest reserves, representing a total of 532 tree species in 44 plant families. The results of this project are described by Coutinho (in prep.).

The need for a phenological study became evident for the phase II of the genetic reserve implementation project. However, the large number of tree species found in the eight forests surveyed brought a dilemma over the number of species to study. Although the study of a large number of trees of only one to few species is the norm in forestry research aimed at tree improvement, for 'in situ' conservation of genetic resources it was clear that a much larger number of species was needed. The first problem was to decide where to draw the line when choosing a number of species appropriate to the time and resources available. Too large a number of species would result in a smaller number of individuals per species being studied, but too
few would not allow relevant ecological conclusions. Having accepted that only a fraction of the total tree species could be studied, the second problem was to decide which species to include in the project. With the advice of Prof. G. T. Prance, the following criteria were adopted:

i) Species from well-studied plant families with monographs and specialists that could help with identification;

ii) Species which occurred in several of the study sites;

iii) Congeneric species occurring in the same locality;

As a result, 15 plant families and 139 species of trees were selected. Table 5.1 shows the plant families selected as well as the number of genera and species within each one.

3.2. SAMPLING TECHNIQUES

Many of the early phenological studies of tropical trees were carried out using only one individual per species. Other studies which included more than one individual per species presented conclusions about a species' phenology without quantifying proportions of individuals exhibiting each phenological phase. Although there is no precise criterion on how many individuals per species are necessary
for phenological studies Frankie et al. (1974a) suggested that a minimum of five trees per species should be observed.

Based on the results of the surveys conducted in the eight forest sites it was decided that each tree species of each site should be represented by eight individuals whenever possible. Thus, for each forest studied eight individuals of each of the selected species were randomly drawn by a computer program developed in Basic. As a result, whenever a surveyed site had more than eight individuals of a certain species, the individuals were chosen randomly. In the cases where less than eight individuals of a species occurred at any site the entire population was included in the study. This means that a common occurring tree species could be represented by a much larger number of individuals. A total of 1508 individuals of the eight forest sites were selected for the phenological study.

Botanical documentation carried out during the course of the study revealed that 34 trees had been wrongly identified. Of these, 23 were later correctly placed in 19 species while 11 trees remained unidentified. These trees were maintained for the community level analysis but were excluded from the species level analysis.
3.3. TAXONOMY OF THE SPECIES STUDIED

3.3.1. Documentation

The species included in this project were documented by a large number of botanical voucher collections. For the taxonomically difficult groups or species every individual included in the study was collected. For the more common species a minimum of one individual per site per species was collected. Exception was made for the two palm species studied which had each only one collection. All individuals with questionable identification were excluded from the species study. The voucher materials of this study are listed on the Appendix I and are deposited in the Herbarium of the Royal Botanic Gardens, Kew.

3.3.2. Determination

The provisional field determination of the species studied were double checked by specialists of each plant family or group. Duplicates were donated to each institution where the determinations were carried out. The thorough examination of the botanical materials by the specialists revealed 'a posteriori' that some complex genera such as Inga, Licania, Eschweilera and Trichilia included many more species than were previously thought by our field identifications. Concomitantly local variation which led us to place two populations as distinct species turned out
to be the same species. For these reasons the original sample of individuals/species/site became reduced or enhanced for some tree species.

3.4. PHENOLOGY DATA

3.4.1. Data Collection

The 1508 individuals selected for the phenological study were flagged to facilitate their location among the other individuals trees of each reserve. Their canopies were observed monthly with the aid of binoculars and the phenology phase recorded in pre-prepared field data sheets. The observations were recorded for 36 months, from May 1987 to April 1990. The first 18 months of observations were carried out personally by this researcher, while the rest was obtained by another technician assisted by two members of the same crew that assisted during the first 18 months of field work. A system of nine codes was devised to facilitate the recording of the various phases. The codes used in the field were: (1) Canopy complete/old leaves; (2) Canopy partly defoliated; (3) Canopy totally defoliated; (4) Canopy flushing; (5) Canopy complete/new leaves; (6) Flowering; (7) Fruiting; (8) Canopy defoliated and flowering; (9) Canopy with old and new leaves.
3.4.2. **Statistical Analysis**

The raw data of phenological codes of each tree were stored and analysed in a personal IBM compatible computer through the program DBase III+ by Ashton-Tate. The original nine codes devised were rearranged and simplified to six phases:

1. Old Canopy
2. Shedding
3. Flushing
4. Entire new canopy
5. Flowering
6. Fruiting

The summation of the phenology of each tree species as well as of each forest site was transferred from PC diskettes into an Amdahl-5890 computer of the University of London Computer Centre, where they were analysed by means of the Statistical Analysis System (SAS), Version 5.18.

The plots on flowering and fruiting phenology of tropical trees given in Chapter 5 show that their distribution was positively skewed and thus the representativeness of the sample mean would not be satisfactory due to being removed from the main concentration of frequency. Therefore, for a more meaningful comparison of several phenologies the median was chosen instead, since it represents the central value when the observations are arranged in numerical order. For this reason strict analysis of variance (anovar)
is not appropriate for phenology data and non-parametric analyses of variance was chosen instead.

3.5. SOIL STUDIES

3.5.1. Sampling

At each forest site studied several pits of 0.8 to 1.0 m deep were opened on undisturbed areas on both sides of the transect. Two to three pits of each forest were then selected for study. The profiles were examined and samples were collected from each visible soil layer, namely A, B and C, at 15, 40 and 75 cm respectively. Only samples of visible layers, and, at the 'várzea' forest only the top layer, were collected since the area was beginning to be inundated at the time of soil collection.

Each soil sample collected received a sequential number cross-reference with the field notes. The soils were taken to the laboratory and oven-dried at 40°C as is normal in areas of very high humidity such as those that occur near the Equator, and can be considered equivalent to air drying. After drying, a subsample of the soil was separated and packaged to be shipped to the Brazilian National Soil Survey and Conservation Service (EMBRAPA-SNLCS) in Rio de Janeiro, from where it was reshipped to University College London’s Biology Department, where the physical analyses took place. The chemical analyses were carried out in the Tropical Soils Analysis Unit of the ODNRI, in Reading.
3.5.2. Physical and Chemical Analyses

The following analyses were performed on the soil samples:

1. Particle size
2. pH
3. Percentage of organic matter
4. Total Nitrogen
5. Extractable Phosphorus
6. Total Phosphorus
7. Exchangeable bases (Ca++, Mg++, Al++)
8. Cation exchange capacity (CEC)
9. Effective Cation exchange capacity (Ef.CEC)
10. Exchangeable Aluminium
11. Total Aluminium

The discussion of the above tests are as follow:

1. **Particle size.** Particle size analysis was carried out by the Hydrometer method. 50 g of the 40 QC dried soil samples were placed into a blender cup with 300 ml d. water and 5 ml of Sodium Lauryl Sulphate as a dispersing agent. The contents were mixed in the blender for ten minutes and poured into a 1,000 ml measuring cylinder. The blender cup was rinsed with 400 ml d. water and the washing put also into the cylinder. A hydrometer was then carefully inserted into the cylinder and additional d. water was added so that the water line marked 1,000 ml. The hydrometer was removed
and the cylinder shaken vigorously by covering the end and turning it upside down, and then let set for three minutes. A reading of the hydrometer was taken after four minutes and the temperature recorded. After two hours the hydrometer was reinserted, left for four minutes and then read. The temperature of the soil solution was recorded. The calculation of the particles was done in the following manner:

\[
\% \text{ Sand} = 100 - \frac{\text{hydrometer reading at 4 min.}}{\text{weight of soil}} \times 100
\]

\[
\% \text{ Clay} = 100 - \frac{\text{hydrometer reading after 2 hr.}}{\text{weight of soil}} \times 100
\]

\[
\% \text{ Silt} = 100 - (\% \text{ sand} - \% \text{ clay}).
\]

These categories are defined in the International scale as:

- sand 2.0 - 0.02 mm
- silt 0.2 - 0.002 mm
- clay < 0.002 mm

2. pH. About 20 cubic cm of soil was placed in 50 ml beakers to which 20 ml of d. water was added. The soil solution was stirred with a magnetic stirrer for a few minutes and allowed to sit for 10 minutes. The electrode of a previously calibrated pH-meter was immersed into the beaker, and the pH value was recorded to the decimal place.
3. **Percentage of Organic Matter.** The total organic matter determination was carried out by the loss on ignition method. Ten g of 105 QC dried soil samples were placed into weighed and numbered crucibles and placed into a 375 Q C oven for four hours. The crucibles were cooled into a dessicator and reweighed. The result was obtained by subtracting the weights of the ignited soil samples by the weight of the 105 QC dried soil samples.

4. **Total Nitrogen.** Total Nitrogen was determined in an auto-analyzer by the micro-Kjeldahl method. 0.1 g of finely ground soil was digested inside test tubes with sulphuric acid and selenium at 360 Q C so that soil organic nitrogen was reduced to ammonia. This temperature was obtained by using a ratio of 1:2 w/v sodium sulphate (Kjeldahl tablets) to sulphuric acid. The ammonia was absorbed in the excess sulphuric acid, producing ammonium sulphate. A set of working standards of known concentration and two blanks were used. A composite factor was obtained from the Optical Density (OD) of the standards. From the Optical Density of each soil sample the value obtained from the blanks was subtracted and the result multiplied by the composite factor. Calculation:

\[
\text{ppm N in sol.} \times 20 \text{ ml} = \mu g \text{ N in 0.1 g}
\]

\[
\text{ppm N} \times 20 \times 1,000 = \mu g \text{ N in 100 g.}
\]
Or:

\[ \text{ppm N} \times 20 \times 1,000 \]

\[ \% N = \frac{\text{ppm N} \times 20 \times 1,000}{1,000,000} \]

5. **Extractable Phosphorus.** Phosphate was determined by the auto-analyzer, using ammonium molybdate as a reagent.

6. **Total Phosphorus.** Total Phosphorus was determined in the auto-analyzer after digestion of finely ground soil by perchloric acid.

7. **Exchangeable Bases** (Na\(^{+}\), K\(^{+}\), Mg\(^{++}\), Ca\(^{++}\)). The exchangeable sodium, potassium, magnesium and calcium were extracted from the soil samples by leaching them with 1 M ammonium acetate. The determination was carried out on an Atomic Absorption Spectrophotometer (AAS).

8. **Cation Exchange Capacity** (CEC). The CEC was determined by an auto-analyzer. This extraction followed the exchangeable bases extraction on the same funnels of soil and sand. The exchanged ammonium ions were replaced in the soil by leaching with 1 M potassium chloride at pH 2.5. The ammonia was determined colorimetrically.

9. **Effective Cation Exchange Capacity** (Ef.CEC). The effective CEC is the CEC as it occurs in the field. The field values for CEC are slightly different in soils with high aluminium content and low pH, which is the case of the Jari soils. The Ef.CEC was calculated by dividing the value
of the exchangeable bases by itself plus the aluminium, multiplied by 100.

10. **Exchangeable Aluminium.** The exchangeable aluminium was also done on the AAS. 90 ml of the 1M KCl extracting solution was made up to 200 ml with distilled water.

11. **Total Aluminium.** Total aluminium was determined by the AAS at 309.3 nm, using a nitrous oxide/acetylene blue flame.
4.1. HISTORICAL ASPECTS OF PHENOLOGY

The distinction between the reproductive and vegetative phases of plants has been dealt with early in the history of modern Botany. Linne’s 1753 ‘Vernatio Arborum’ can probably be considered the first study of tree phenology of modern times. Linne was to repeat his preoccupation with the influence of the seasonal changes upon plants and animals in several of his dissertations. For example, in ‘Calendarium Florae’ (1756) he utilized nature’s signs to subdivide the calendar year and in ‘Coloniae Plantarum’ (1751) he discoursed about the dispersal agents of plants mainly wind, water and human. Darwin (1859) explored the competition for pollinators and the onset of flowering in male and female plants of the same species.

Some of the early studies in phenology were carried out in botanic gardens or other type of plantation (i.e. Robertson 1895, Salisbury 1921, 1942). Robertson (1895) observed 488 insect pollinated plants including 18 trees and interpreted the results in relation to plant taxa distribution. Dingler (1911) reported the phenology of 18 species of tropical trees growing at an experimental station in Ceylon.

Foresters at the beginning of this century have recognised the importance of the adaptations shown in the vegetative cycle of trees, and concentrated their work on factors such
as seed dispersal, germination, seedling establishment and leaf shedding (e.g. Dingler 1911, Simon 1914, Schweizer 1932). Today it is widely accepted that the stages preceding seed dispersal, such as flowering and fruiting are important to the understanding of genetic systems of populations. The physiological processes related to flowering and fruiting are thought to be necessarily adapted to both the abiotic (climate) and biotic aspects of the region where evolution occurred. Variables found in the local environment can be used to improve models of flowering and fruiting phenology.

The simultaneous development of ecology, genetics and physiology and the application of these subjects to Forestry and Agriculture encouraged the systematized pursuit of phenological data after the second half of the present century. Many such studies were carried out in the northern hemisphere, particularly in those Scandinavian countries which have a significant forest industry such as Sweden, Finland and Norway (Stern & Roche 1974).

The most comprehensive treatise on phenology to date is Lieth’s Phenology and Seasonality Modeling (1974). A further review on the subject was in 1985 by Rathcke and Lacey. Both demonstrate the state of the art in Phenology.

In the United States, the interest in this subject led to the establishment of a Phenology Committee linked to
UNESCO's (United Nations Educational and Scientific Organization) International Biological Program (IBP). It pointed out the need for ecosystem orientated phenological study on a worldwide basis. A symposium on this subject was held in August 1972, during the 25th Annual Meeting of the American Institute of Biological Sciences (AIBS) in Minneapolis, Minnesota (Lieth 1974).

Despite this increase in interest, we still know very little about the phenology of tropical and subtropical tree species (Stern & Roche 1974, Frankie 1975, Augspurger 1983). In the tropics most of the work was done in Asia and Africa, mainly in countries which until recently were colonies of European powers. In the neotropics most developments in this field have taken place in recent ex-colonies, such as the Guianas and West Indies and in areas under the direct or indirect influence of the United States such as Hawaii, Puerto Rico, Panama Canal Zone and Costa Rica.

A major finding of the phenological studies carried out in the tropics and sub-tropics is that even the small climate changes that take place there control the various phenological cycles of plants. Reports in the literature state that most neotropical areas of altitude below 1000 m show some kind of dry season, that is, a period of distinctly reduced rainfall. Some areas, mainly in Central America, show two periods of low rainfall, a short one in
July-August, which is named 'veranillo', and a longer one, December-May, the true 'verano'. Even the most humid forests seem to have some kind of drier period, however slight the decrease in precipitation may be, with some influence upon the flowering and fruiting periods. At a first glance, the photoperiod may not seem to be a significant factor over the control of flowering in the tropics, where the difference between the longest and the shortest day of the year is only 55-65 minutes (Murashige 1966). But this is not so. Having fewer overcast days, the dry season has more hours of sunshine than the rainy season and thus greater insect activity. Janzen (1967a) sees this as a selective force for the dry season being the peak period of tree flowering in the tropics.

4.2. EVOLUTIONARY ASPECTS OF PHENOLOGY

There are few models of studies in tropical plant evolutionary ecology utilizing scientific methodology. In the case of tropical phenology the situation calls for more systematic studies. According to Howe (1985) the literature characterizes itself by a plethora of concepts, assumptions, hypotheses, arguments and biased interpretations of evidence. For instance, the phrase 'selective forces' has been used and abused in order to explain both the occurrence and the non-occurrence of the same phenomena. Howe (1985) has criticized many of such untestable and thus unrefutable explanations that clutter the literature. He mentions other authors who share the
point of view (Williams 1966, Gould and Lewontin 1979 and Lewontin 1965, in Howe 1980) and stresses that such "... unrestrained ad hoc reasoning has been levied at students of adaptation". He brought the discussion foward by defining the terms most used and misused in evolutionary ecology to relate time and mode of dispersal (Howe 1982, 1986a).

According to some ecologists (Janzen 1967a, Gentry 1974, Borchert 1983) the reproductive phenology of plants can be considered the result of coevolution of trees with pollinators and seed dispersers/predators. Thus, the peaks of flowering are related to periods of high pollinator activity. Other ecologists relate the patterns in flowering and fruiting to environmentally controlled mechanisms analogous to those that temperate plants evolved in order to adapt to vegetative and reproductive development during a limited growing season (Larcher 1980, in Borchert 1983).

Janzen (1967c) has postulated the occurrence of selective forces behind the dry season peak of reproduction in tropical America. He suggests one should look for the many advantages or disadvantages to flowering and fruiting during the dry period as compared with the rainy season, rather than to direct environmental conditions such as moisture. The first condition he analyses is competition, such as for sunlight between canopies. He points out that while isolated forest trees seem to show flowers and fruits uniformly around their canopies, trees occurring within a
continuous forest canopy tend to flower only on branches that are not shaded. He suggests that during the wet season selective forces would be those that maximize photosynthetic activity for vegetative growth in order to reduce shading, rather than the direct use of such photosynthetic activity in reproduction. Flowering in a burst could also be advantageous for both the pollinator and tree. He discussed many characters in both dry and wet season that could influence flowering, as summarized in Table 4.1.

Janzen (1971) also reappraised the various aspects of seed predation by animals. A hypothesis he offered is that the seed must escape from the predators at the seed crop and in the parent's habitat, before and after dispersal to ensure the next stage of seedling establishment. In other words, when a seed is released by the parent to the ground, for instance, its mostly likely fate is to rot or to be preyed upon, unless it is removed by a dispersal agent. Evidence for this hypothesis have came from studies in Virola (Howe 1986b), Dipteryx (Clark & Clark 1984) and other species cited by Clark & Clark (1984) showing that seed and seedling mortality was proportionately higher near the parent tree than far from it.

It has been reported that many tropical animals depend on fruit for food and that a large percentage of tropical trees bear fruits adapted for animal consumption (Howe 1984). Pollination and seed dispersal by animals are
considered forms of nonsymbiotic mutualism, since organisms enhance each other's fitness but do not live together (Howe 1983a). Howe points out that a distinction should be made between facultative and coevolved mutualisms. According to him, the question to be asked is whether coevolution shapes the attributes which mediate mutualism or whether variation in ecological factors promote facultative rather than coevolved mutualism (Howe 1983a).

It is the role of evolutionary ecology to look for the factors that influence pollination and dispersal, and to decide whether variations in relative success are genetical adaptations from within the plant itself or a response to environmental conditions (Howe 1982). The reproductive phenologies of trees are thought to be of evolutionary significance because of their interactions with pollinators and dispersers. Rathcke & Lacey (1985) presented a hypothesis about the possible evolutionary causes and consequences thereof of the differences encountered in phenological patterns. The role of competition for pollinators to enhance reproduction and thus fitness have also been tackled by a few researchers.

Although a large number of phenological studies of tropical trees have concluded that it is the environmental factors such as rainfall and photoperiod which control phenology (Alvim & Alvim 1978), there are also many that claims that flower induction in tropical trees is under endogenous control and affected only indirectly by environmental

Gentry (1974,1982) studied the phenology of bee pollinated Bignoniaceae, mainly lianas, from Central America, and devised five types or patterns of flowering (Table 4.2.). He considers competition for pollinators as a possible selective pressure from which result diverse phenological patterns. To him the different strategies observed have an important role in making effective competition for the same pollinator amongst the many related species (Gentry 1974).

Table 4.1. Selective Forces for Seasonal Peak Flowering in the Tropics (Adapted from Janzen 1967a).

<table>
<thead>
<tr>
<th>Dry Season Characters</th>
<th>Selective Forces</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Positive</strong></td>
<td></td>
</tr>
<tr>
<td>Lack of rain</td>
<td>1. Prevents knocking off flowers</td>
</tr>
<tr>
<td>Drier air</td>
<td>2. Prevents dilution of nectar</td>
</tr>
<tr>
<td></td>
<td>3. Avoids flooding insect holes</td>
</tr>
<tr>
<td>Leaflessness</td>
<td>4. Concentrates the nectar</td>
</tr>
<tr>
<td></td>
<td>5. Facilitates the drying of seeds with pods</td>
</tr>
<tr>
<td></td>
<td>6. Facilitates explosive dehiscence of fruits</td>
</tr>
<tr>
<td>Bright colours of flowers and fruits</td>
<td>7. Reduces fungal activity</td>
</tr>
<tr>
<td></td>
<td>8. Facilitates the location of flowers and fruits by pollinators and dispersers</td>
</tr>
<tr>
<td></td>
<td>9. Promote the visual orientation of pollinators and dispersers</td>
</tr>
<tr>
<td><strong>Negative</strong></td>
<td></td>
</tr>
<tr>
<td>Lack of water in soil</td>
<td>1. Rapid wilt of flowers</td>
</tr>
</tbody>
</table>
### Table 4.2. Patterns of Flowering Phenology (From Gentry 1974)

<table>
<thead>
<tr>
<th>TYPES</th>
<th>NAME</th>
<th>POLLINATOR(S)</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Asynchronous</td>
<td>Bat, wasp</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>Steady-state or extended</td>
<td>Bee</td>
<td>Few flowers/day, one or more/month</td>
</tr>
<tr>
<td>3.</td>
<td>Cornucuopia</td>
<td>Various</td>
<td>Lge. nQ fls. &gt; several weeks</td>
</tr>
<tr>
<td>4.</td>
<td>Big-bang or mass blooming</td>
<td>Bee</td>
<td>Much synchronization, fls. few days/yr.</td>
</tr>
<tr>
<td>5.</td>
<td>Multiple-bang or episodic fl.</td>
<td>Bee</td>
<td>Short flowering per. (2-3 days) scattered thro' yr.</td>
</tr>
</tbody>
</table>

Besides Gentry's study in the phenology of Bignoniaceae (Gentry 1974) the only other phenological study concerning a plant family is that carried out by G.T. Prance and S.A. Mori in Lecythidaceae, published in Prance and Mori (1971) and Mori and Prance (1987a). The first one, by Prance and Mori (1971), identified three types of flowering strategies in Lecythidaceae and reported staggered flowering in several congeneric sympatric species such as Corythophora alta and C. rimosa (Prance and Mori 1971). The second study, Mori and Prance (1987a) was concerned with the phenological comparison of similar species of Eschweilera. They cited Eschweilera decolorans and E. laevicarpa, similar species living in identical habitats, with overlapping flowering phenology. This study concluded that a phenological separation in similar species did not always occur (Mori & Prance 1987a).

The phenology of six species of *Annona* shrubs to trees...
found in various states of Brazil, including Amazonas, was reported by Gottsberger (1989) from observations between 1977 and 1986. All six species were found to flower in a staggered fashion during the rainy season, from October to January (Gottsberger 1989).

The phenological studies in the tropics can be classified into three types: (1) those carried out by amalgamating leaf, flower or fruit debris of many species within a forest community (Foster 1974, Jackson 1978); (2) those which studied one to few species represented by many (>10) individuals (Magalhães & Alencar 1979, De Steven et al. 1987, Alencar 1988); (3) those which studied several species represented by few (<10) individuals (Daubenmire 1972, Alvim & Alvim 1978, Magalhães 1982). The literature has many other accounts of descriptive phenology of tree species without any quantification at population level, but these will not be considered here. Very few comparative studies have been carried out within one family or within one genus, and fewer have focused on populations and their individuals (Augspurger 1983).

Most studies in the tropics have shown that tree flowering is strongly seasonal and that it usually coincides with the period that the tree has lost at least part of its leaves. The literature has also shown that not all trees flower annually. Some may flower more than once in a year, while others may flower pluriannually. It is thought that climax species tend to flower once a year and synchronously while
pioneer species tend to flower more continuously (Whitmore 1990). Another common feature reported is the flowering independence between branches of some large trees (Schnell 1970).

4.3. FOREST TREE PHENOLOGY IN THE PALEOTROPICS

Jean Schweizer, between 1925 and 1932, studied the phenology of the cultivated rubber tree, Hevea brasiliensis, on the island of Java, which was then part of the Dutch East Indies (Schweizer 1932). He found that cultivated Hevea flowered and fruited asynchronously, and that such differences occurred even among individuals of the same clone (Schweizer 1932).

The most extensive tropical phenological study was carried out by Koelmeyer, in Ceylon. He studied the phenology of 2,000 trees of 125 species over nearly 10 years, comparing several types of forests (Koelmeyer 1959 in Foster 1974).

The second most extensive study in tropical phenology was carried out during 1960-69 by McClure (1966) and Medway (1972) in a Dipterocarp Forest in Malaya, Malasia, and is one of the most frequently cited. It involved 45 species represented by 61 canopy trees, which were observed from a 43 m platform built at the branches of an emergent dipterocarp. Observations were carried out at intervals of 5-30 days. In spite of the importance of this study, its
low number of trees per species did not allow extrapolation on reproductive synchronization of the species involved. Out of the 45 species, only ten flowered every year. At least 20 flowered and 12 fruited each year. Leaf growth (flushing) showed two seasonal peaks, with a more marked one coinciding with the less pronounced wet season and a less marked one coinciding with the main rainy season. One chrysobalanaceous species, *Licania splendens* (Korth.) Prance & Kosterm., produced fruits in 1961, 62, 63, 65 and 68, with flowering occurring in April-June and extended fruiting until November (Medway 1972; McClure 1966).

Shukla and Ramakrishnan (1982) observed 122 tree species of a sub-tropical forest in northeastern India, at intervals that ranged from two weeks to one month. They plotted their data according to the number of species showing each phase. The phase category adopted for each species was the one to which more than 50 per cent of its individuals could be assigned. Leaf fall was the phase best correlated with climatic events, and it was more intense in the middle of the dry season. Flowering did not show any seasonal pattern as had been reported in other studies, but maximal activity was seen during the warmer period that coincides with the beginning of the rains. A peak fruiting time occurred during the wet season.

Another phenological study in India was carried out in six sites of different altitudes of the Kumaun Himalaya forest, by Ralhan et al. (1985). At each forest a plot of one
hectare was selected on which 20 randomly chosen individuals were selected for each of the 54 species studied. The records were gathered from January 1981 to December 1982, at 4 or 5 day intervals, during the period of high activity, and 3 or 4 weeks during the rest of the year. Flushing was confined to the autumn and winter for the deciduous species, and to spring and summer for the evergreens. It was separated into two groups, according to whether it occurred as one-time or as a multiple event. The authors suggested that the latter could be an evolutionary strategy to enable a more efficient utilization of favourable periods within an unfavorable season, and could function as a protective measure to ensure the presence of some leaves following a catastrophic climatic change or insect attack. Almost all of the species studied flowered during the dry season. The reproductive 'clock' of most of the species studied seemed to be set during the interphase between winter and spring (early summer), in order to take advantage of the summer rainfall for productivity and recruitment of new individuals through germination. They concluded that despite the differences in altitude, all six forests studied showed similar phenological activities (Ralhan et al. 1985).

An elegant but short study was recently completed in India by P. Newton (1988), in which he monitored 215 trees of 61 species during 14 months. The studied area, a moist deciduous forest in Madhya Pradesh shows three seasons: cold-weather (Nov-Feb), hot-weather (Mar-Jun) and monsoon
(end Jun-Sep). The majority of the species studied appeared to follow a simple annual cycle, with reproduction occurring during the hot weather deciduous phase. His paper also reviewed seven other phenological studies in South Asia, all of which showed a pattern of dry season leaf fall followed by flowering and flushing. He attributed the flowering to a lower water status (dehydration) resulting from leaf fall.

An important contribution to phenology in Tropical Africa was published in 1982 by D. Lieberman. Her work was carried out on a tropical forest and in a grassland/thicket mosaic, in Southeastern Ghana. The area studied exhibits two dry seasons, one in December-February and the other in August-September. The reproductive status of seventy-nine species of trees, climbers and shrubs, represented by 'a large number of individuals' were observed every ten days from December 1976 to April 1979. The girth increase of 12 species (114 trees) were also measured by dendrometers or by a dial caliper. Her results showed a peak for flowering and fruiting during the period of higher rainfall. The reproductive phases of the forest trees and shrubs followed this pattern, with 11 per cent flowering during the dry season versus 78 per cent flowering during the wet season. The separation of the fruits of all species (trees, climbers, shrubs and herbs) into dry and fleshy types showed a rather large number of fleshy fruits maturing during the wet season, while the dry fruits seemed to mature mostly during the dry season. As far as leaf fall is
concerned, the deciduous species shed their leaves mostly during the dry season. About 19 per cent of all forest species (trees, climbers and shrubs) became leafless, compared with 55 percent of the 42 grassland-thicket species.

4.4. FOREST TREE PHENOLOGY IN THE NEOTROPICS

According to a review done by Janzen (1967a) until the mid-sixties there has been only one study on flowering and fruiting records for a single major site in Central America, which is described by Allen (Janzen 1967a). Allen's data consist of flowering and fruiting records of 288 tree species of deciduous and semi-deciduous forests in Costa Rica, based on five years of residence in the area and on herbarium sheet records. The area had a major dry season from March to April and a minor one during late November and early December. A flowering peak (97 species) occurred in February, with a fruiting peak (51 species) in March. Of the 288 species, 44 fruited one-half month or more apart. Some species showed flowering or fruiting for an extended period of 6–12 months of the year. Leaf dehiscence was gradual, but nearly complete on the ridges of the hills during the dry months.

Janzen (1967a) also reviewed the results of another study in the same area, in which out of a sample of 10-67 trees, only 5.4 percent of the individuals and 35.5 percent of the 85 species studied were in flower or fruit in July 1966.
Mathias 1966 in Janzen 1967a). This figure showed also that a large number of individuals do not undergo a reproductive phase in some years. A detailed study on tree flowering periodicity in Central America (Fournier & Salas 1966), also showed that a major peak was present during one such dry season (December-March) for 100 species.

Foster (1974) studied fruit production in a Panama forest by sampling seed and fruits that fell in the forest floor with the use of 0.83 square metre traps arranged in 24 plots. The seeds were identified to species and then counted. Two peaks of fruiting were found: one during the transition from dry to rainy season (May-June) and another in the later part of the rainy season.

So far the most extensive phenological study in Tropical America is the one by Frankie, Baker and Opler (1974a). They compared the phenological responses of trees in tropical wet and dry forests of Costa Rica. A total of 1,137 trees separated into wet and dry sites were included in this study. The number of individuals observed was 468 for 185 species in the wet site (2.5 individuals per species) and 669 for the 113 species in the dry site (10.2 trees per species). Their observations were made from November 1968 to December 1970 (25 months) for the wet site, and from April 1969 to July 1970 (15 months). Eleven species were found in both sites, five of which showed similar flowering and fruiting behaviour. Trees were separated according to whether they were overstorey or
understorey, and whether they were common or rare. Their results showed that in overstorey trees leaf drop peaked in February (dry season), although it had begun during the wet season. Understorey trees had almost negligible leaf fall compared to overstorey ones. Leaf flushings peaked with the middle portions of the two dry seasons (February and September), with less in the latter season. A great number of all the species studied (85 out of 113) lost their leaves at least partially while 17 per cent remained evergreen. Their blooming behaviour was divided into two categories: (i) seasonally-flowering species which bloomed in either or both the dry and wet seasons, and (ii) extended-flowering species, which bloomed over two or more consecutive seasons. About 12 to 14 percent of the species of over- and understorey, respectively, showed unsynchronized flowering. Seasonal and extended fruiters were also found to have the same pattern as for flowering. A single peak in fruiting activity was seen in April (end of dry season). From June to November the production of mature fruits remained low but constant, with seven to thirteen species in fruit during any month. The mean flowering time was 5-6 weeks, and almost all dry-site species showed intrapopulation synchronization. Twelve species showed variation in flowering pattern between the years of observations. The dry site showed twice as many 'seasonally' flowering species in bloom as the wet season (Frankie et al. 1974a).

Daubenmire (1972) studied leaf senescence, leaf production,
flowering and the dissemination as well as the trunk radial increment of 41 trees of 25 species, in the Gaunacaste Province, Costa Rica. His data were recorded weekly during 12 months. The objective of this study was to characterize the tree stratum of three forest types: a savanna forest, an upland forest and a riparian forest for any possible comparisons with deciduous temperate zone forests. He found that new leaves were formed throughout the year, except during the last two thirds of the dry season, and that the highest percentage of species losing their leaves synchronously occurred during the middle of such dry season. Slightly less than half of the species were deciduous, and an appreciable number of the species were semideciduous or semievergreen. He found that the peak of flowering coincided well with the period when the canopy was most nearly leafless, which could occur at both the dry season and during the 'veranillo'. Only three species flowered during the rainy season. When the pollination and the dissemination vectors of these forests were compared with those of a deciduous temperate one, he found the pollination in the former was carried out entirely by animals (mainly bees), with their major seed dissemination vector being wind, while the temperate deciduous forests showed a reverse situation.

Stiles (1977) studied 11 hummingbird pollinated non-tree species (Heliconia spp.) in a Costa Rican rain forest, for a four year period. He concluded that flowering occurred in a steady sequence rather than in an aggregated fashion. In
other words, the flowering peaks were more regularly spaced than would be expected from a random model. He attributed this to competition between plants for pollinating hummingbirds. Poole and Rathcke (1979) challenged Stile's conclusion by using statistical tests to compare the intervals between dates of a flowering peak with intervals between randomly spaced points, and gave an opposing conclusion. Cole (1981) defended Stile's original conclusion based on the fact that Poole & Rathcke's calculation relied on the assumption of a uniform growing season throughout the year. The final consensus was that flowering was largely staggered although the staggering itself was random (Cole 1981).

Croat (1969, 1975) used herbarium collections from Barro Colorado Island in Central Panama to study the flowering and fruiting behaviour of several species of trees (large and small), shrubs and herbs. From his data he separated plant families that tended to flower in the dry and in the wet season, as well as those which flowered all year long. The dry season families: Anacardiaceae, Acanthaceae, Bombacaceae, Cochlospermaceae, Combretaceae, Lauraceae, Marcgraviaceae, Theaceae, Tiliaceae, Turneraceae, Violaceae and Vochysiaceae had mostly woody species, mainly trees. The families that flowered during the wet season had mostly herbaceous species, and all but one were monocots. Although we cannot use his findings on flowering peaks to compare with data on just trees, he did have interesting results. An almost equal number of species flowered in the dry and
the wet season (139 vs. 133). A larger number of species had a transitional behaviour, that is, utilized more than one season for either flowering or fruiting. He found that over 40 per cent of the species had extended flowering periods, up to nine months long. He detected many bimodal species, which had a second flowering during the wet season. He also reported that his herbarium data showed that two Chrysobalanaceae species, *Hirtella triandra* Sw. and *H. racemosa* Lam. had a trimodal reproductive activity.

Still in Barro Colorado island, a four year study with 13 species of palms, each represented by 10 individuals (mostly), was carried out by De Steven et al. (1987). They found that palms had a rather varied flowering pattern. Most initiated flowering during the rainy season, as opposed to the woody community of the same area which displayed flowering mostly at the end of the dry season (De Steven et al. 1987).

Smythe (1970) noted behavioural changes in caviomorph rodents of Barro Colorado, which he attributed to seasonal variation in the abundance of the fruits that they ate. In order to measure fruit availability through time he placed a series of traps along transects. He applied the Shannon-Wiener entropy equation to measured the diversity of fruit fall.

Hilty (1980) studied the time and levels of flowering and fruiting activity of 164 species represented by 621 trees,
in a premontane aseasonal forest of Pacific Colombia, from April 1972 to June 1973. He separated the results for understorey and canopy trees and compared them with the combined total. In this study, flowering was classified into four types: unimodal, bimodal, multimodal and continuous. Synchronized flowering was not observed.

The first extensive data set on phenology (flowering and fruiting) of a single tropical tree species is of *Guarea rhopalocarpa* Radlk. (Meliaceae) carried out in Costa Rica by Bullock, Beach and Bawa (1983). A total of 38 observations between January 1976 and September 1979 was carried out for the 119 trees (some which were marked later had fewer observations). The importance of this work stems from the fact that *Guarea rhopalocarpa*, like many Meliaceae, is a dioecious species and therefore data was obtained for both male and female trees. They also classified the trees by diameter in order to check age with reproductive response. The results showed that *Guarea rhopalocarpa* i) flowered in nine months of the year, although not continuously and that individuals showed some flowering synchrony; ii) flowering was not recurrent at particular calendar dates, nor after definite intervals; iii) all flowering episodes resulted in fruit set in the female trees; iv) trees did not participate in all episodes and showed varied levels of output; v) male and female plants were not strictly parallel in their reproductive activity, and male trees flowered twice as many times as female trees.
Mori and Kallunki (1976) studied the phenology of *Gustavia superba* in Central Panamá. They arranged three quadrats totalling 77.5 square metres along a stretch of road of 105 metres, so that leaves dropped inside the quadrat could be recorded. There were 36 individuals capable of dropping leaves into the quadrats. *Gustavia superba* lost leaves throughout the year, but had a peak in May. Flushing also occurred throughout the year but showed two small peaks. Flowering resembled the cornucopia or Type 3 pattern described in Table 4.2. and occurred from 16 January to 12 June. In this study fruiting showed a bimodal peak which was interpreted as caused by unexpected water stress at the end of the dry season.

4.5. PHENOLOGY STUDIES IN EXTRA-AMAZONIAN BRAZIL

The first phenological studies in Brazil were carried out in the southern tropical and subtropical areas, early this century. The oldest reference is from a 1923 paper by Hermann von Ihering, and dealt mostly with the defoliation and flushing of trees that were grown in Botanical Gardens (Ihering 1923).

Jackson (1978) studied the phenology of a seasonal low montane forest in Espírito Santo by means of 26 traps of about 1.5 square metres, set 6 m apart from one another along two parallel lines. He collected the leaves and
flowers caught in the traps at 10 day intervals, then dried and weighed the materials. His study did not separate the individuals into taxa and thus the data demonstrate only the patterns of all the species combined. The forest showed a peak of flowering during the dry season. Comparing his results with data from the literature he proposed that leaf-fall and flushing result from the combined effect of moisture and temperature. For instance, forests with the combination of moderate temperature stress and low moisture stress will be found to have maximal leaf-fall in whichever part of the year is more propitious for growing new leaves.

Bittencourt (1981) studied the phenology of *Jacaranda macrantha* through the observation of ten individuals of a larger population occurring in a forest reserve in Espírito Santo. His study included experimentation on pollination and measurements on fruit development. The species flowered during the rainy season and fruited during the dry season.

The phenology and cambial activity of 120 trees of 30 different species were studied by Alvim and Alvim (1978) during three calendar years (Jan 1973 - Dec 75) on a forest near the coast of Bahia which had no predictable dry season. Their study focused on the relationship between phenological events with climatic factors. An unexpected drought which occurred during January-March 1973 is indicated as the cause for a lack of flowering in this period. They found that most species tended to flower at the same time each year regardless of year to year
variation in rainfall. In some species flowering appeared to be strongly correlated with environmental factors such as photoperiod and/or temperature, and hydroperiod stimulus. They also found a group of species whose flowering and fruiting showed no relation to external factors. Flush was found to be triggered by a sequence of wetness and dryness. Their results were presented as mean percentage of species in flower, plotted together with the mean monthly temperature and rainfall of the period studied. No significant differences in flowering were detected from month to month which they attribute to the lack of a defined dry season. They suggested that periodic phenomena in trees are many times linked to environmental changes rather than to endogenous control (Alvim & Alvim 1978).

Mori et al. (1980) carried out a six year study on the phenology of four individuals of Lecythis pisonis Cambess occurring in a forest in Bahia. The individuals observed showed flowering synchrony not only within a given year but between years as well. The importance of this work has to do with the evaluation of the number of reproductive units such as number of flowers per tree, number of stamens per flower, number of pollen grains per anther, number of ovules per ovary and number of fruits produced. The result was that fruit production was comparatively much lower than the number of flowers produced (Mori et al. 1980).

Mori et al. (1982) analysed 14 years of phenological data
from Bahia collected at the same forest studied by Alvim & Alvim (1978). While these latter authors emphasized species response Mori et al. analysed the data at community level. For this they combined the phenological responses of 30 species represented by 120 individuals (four individuals per species). They concluded that all months of the year had some kind of phenological activity although a peak of activity occurred in the spring. No correlation was found between defoliation and the pluviometric regimen but flushing was found to be correlated with defoliation (Mori et al. 1982).

Ramalho and Marangon (1989) studied the phenology of *Melanoxylon brauna* Schott. from a forest near Viçosa, Minas Gerais. Their study was carried throughout six consecutive years, through monthly observation of flowering, fruiting and the state of the canopy. The number of individuals involved in the study as well as the availability of botanical vouchers were not reported. The diagrams of the phenophases are based on percentages of occurrence. Flowering occurred during the dry (and colder) season (Mar-Jun) while fruiting occurred at the beginning of the rainy season.

As mentioned earlier in 4.2. the phenology of six species of *Annona* shrubs to trees found in various states of Brazil, including Amazonas, was reported by Gottsberger (1989) from observations between 1977 and 1986. All six species were found to flower in a staggered fashion during
the rainy season which was interpreted as a mechanism to
diminish competition for pollinators (Gottsberger 1989).

4.6. PHENOLOGY OF AMAZON TREES

One of the first published phenology studies in Brazilian Amazon is that by Araújo (1970) in which the phenology of 36 species of economically important trees represented by 210 individuals was described.

Prance and Mori (1971) reported the phenology of several species of Lecythidaceae trees. Up to ten years of phenological observations was reported for Lecythis usitata (now L. pisonis), Lecythis poiteaui and Cariniana micrantha occurring at the Ducke reserve of the Brazilian 'Instituto Nacional de Pesquisa da Amazônia'. They pointed out that although Lecythis usitata flowers after the dry season leaf shedding not all individuals do so every year. From the five individuals observed one flowered in five out of ten years whilst another flowered in three out of five years. They reported that flowering lasted from 1-4 months, and that the fruits matured 7-10 months after flowering (Prance & Mori 1971). They reported staggered flowering patterns in some closely related sympatric species such as Corythophora.

Falcão and Lleras (1980, 81, 82, 83) and Falcão et al. (1981) published in Acta Amazonica a series of results on
the phenology of several fruit producing trees. The species studied were: *Poraqueiba sericea* Tulasne or umari (Falcão & Lleras 1980), *Pourouma cecropiifolia* Mart. or mapati (Falcão & Lleras 1980), *Couepia bracteosa* Bentham or pajurá (Falcão, Lleras & Kerr 1981), *Couma utilis* Muell.-Arg. or sorva (Falcão & Lleras 1981), *Annona muricata* L. or graviola (Falcão & Lleras 1982) and *Theobroma grandiflora* (Willd. & Spreng.)Schum. or cupuaçu (Falcão & Lleras 1983).

In each of these studies ten individuals were observed for a period of approximately 18 months. The most interesting part of these studies was the quantification of the fruit production in relation to flowering. With the exception of *Pourouma cecropiifolia* the species showed a very low fruit set in relation to the number of flowers initially produced. It was observed that the majority of the species tended to flower during the dry season, between June and October. The authors suggested an endogenous control of flowering and fruiting phenologies.

Prance and da Silva (1975) published a book on the cultivated trees of the area around Manaus, including both native and non native Amazon species. The book which was directed towards the horticultural aspects of trees provided a descriptive account of their flowering and fruiting phenologies. This information was reassembled by Alvim and Alvim (1978) in a histogram showing the percentage of species flowering and fruiting at each particular month, which they used to compare with the phenology of trees of a Bahia forest. The histogram
compiled by Alvim and Alvim cannot be regarded as a mode of phenology for the Amazon since it is well known that trees growing in open areas such as in cultivation can have different phenologies from those found in undisturbed habitats. In addition fifty percent of the trees were exotics not native to the Amazon. It can nonetheless be used to show the seasonal tendency of flowering and fruiting which Alvim & Alvim interpreted as indicative of environmental control of phenology.

Alencar et al. (1979) studied the phenology of 27 forest species, mainly trees, represented by 81 individuals, on monthly observations during four years. He separated the species into the following classes: emergent, canopy, low-canopy, overstorey and understorey.

Magalhães and Alencar (1979) studied the phenology of Aniba duckei Kostermans. Later, Magalhães (1982) recorded the fruiting phenology of 48 native Amazon trees growing in farm holdings near Manaus.

Ayres (1986) studied the phenology of 982 trees and lianas that produced fruits that were eaten by the uakari monkeys, occurring in a 'várzea forest'. The study site was located between the rivers Japurá and Amazon. In this study he reported the occurrence of one fruiting peak per year.

As mentioned earlier in Chapter 4 Section 2, Mori and Prance (1987a) observed the phenological responses of 26
species and 210 individuals of Lecythidaceae in an area near Saúl in French Guiana. They found that all the species studied except for the typically 'várzea' species *Gustavia hexapetala* flowered entirely within the dry season or during the transition from the dry to the wet season. The percentage of species in flower at each observation period during the dry season of 1982 ranged from 16 percent to 39 percent. They also found seed drop to be correlated with the onset of the wet season (Mori and Prance 1987a).

Sabatier (1985) described the seasonality in flowering and fruiting phenologies found in a forest in French Guiana. In this study he also compared the fruiting phenology of seven sympatric species of *Eschweilera*. Sabatier & Puig (1986) studied 1130 individual trees of DBH over 5 cm, by direct observations during certain periods of the year (February-March and August-October), from 1978-1981. They also sampled the forest litter in order to measure the flower and fruit production of a population estimated in 1900 trees of DBH over 2 cm. They proposed the following models of flowering and fruiting: continuous, discontinuous, pluriannual and regular or irregular. They found flowering to be generally synchronous among individuals of the same species. No difference was found in the timing of fruit maturation or dehiscence between canopy and understorey species, although authocorous and anemochrous species were found to be more seasonal in fruiting production than zoochorous species.
Daly (1987) noted the phenology of 12 species of Protium that occurred in the Mocambo reserve, in Pará. He found that flowering was not spread and occurred in two distinct peaks, one in October-November and the other one in March, coinciding with the beginning and end of the rainy season. Some displacement was found by means of the strata occupied by each species. However, displacement and reproductive isolation by means of selection for, or coevolution with, different pollinators cannot be easily deduced in Protium. In Mocambo, the only species which strongly suggested a different pollinator from the rest was Protium subserratum, that had free petals that are erect at anthesis, and long ascending hairs found on its adaxial surface.

To the present the largest sample of a single Amazon tree observed for phenology was carried out by Alencar (1988) involving the study of 82 individuals of Copaifera multijuga Hayne, in the Ducke forest reserve near Manaus. In this seven year study the results of the phenology phases studied was given in terms of percentage. Results showed that Copaifera multijuga reproduced at every two years and even so with less than fifty per cent of the individuals flowering. In this species flowering took place during the rainy season contrary to most species so far studied (Alencar 1988).
CHAPTER 5. RESULTS: SPECIES PHENOLOGY

One of the recommendations formulated during the concluding session of the 1968 Linnean Society Symposium on 'Speciation in the Tropics', was that studies on tropical seasonality should be carried out on a species by species basis in order to allow for generalizations to be made on higher taxa (Cain 1969). This section describes quantitatively the phenology of the 137 tree species studied, arranged alphabetically according to their botanical family. This arrangement may allow inferences of phenological patterns at generic or family levels. Further in Chapter 8 a distinction is made between model of species phenology and model of individual tree phenology. Most phenological models or patterns described in the phenological literature refer to the phenology of individuals. The phenology models given in the various family tables found in the present chapter refer to species patterns resulted from the observation of its population.

Throughout this chapter the phenological details refer to the three years of study and not to the four calendar years that were involved. The monthly indices used in Figures 5.1 - 5.96 are displayed in Table 5.1. The symbols utilized in the same figures are listed in Table 5.2.
Table 5.1. Key to the monthly indices used in Figures

<table>
<thead>
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<th>INDEX</th>
<th>MONTH</th>
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<tr>
<td>1-8</td>
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<tr>
<td>9-20</td>
<td>January-December</td>
<td>1988</td>
</tr>
<tr>
<td>21-32</td>
<td>January-December</td>
<td>1989</td>
</tr>
<tr>
<td>33-36</td>
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Table 5.2. Key to the figure symbols

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<th>SYMBOL</th>
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<tr>
<td>Ø</td>
<td>Fruiting</td>
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<tr>
<td>⬤</td>
<td>Old Canopy</td>
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<tr>
<td>△</td>
<td>Leaf Shedding</td>
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<tr>
<td>+</td>
<td>Flushing</td>
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<tr>
<td>❌</td>
<td>Entire New Canopy</td>
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Table 5.3. Families of trees studied.

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<th>NO SPECIES</th>
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<tr>
<td>CHRYSOBALANACEAE</td>
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<tr>
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<td>1</td>
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</tr>
<tr>
<td>HUMIRIACEAE</td>
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</table>

* Not included in the species study of this chapter.
The Anacardiaceae is a worldwide family comprising 74 genera and over 600 species of trees, shrubs and woody climbers, mostly common in the tropical and subtropical regions, with a few inhabiting temperate zones (Mitchell 1987). There are 25 genera which have arborescent species although only two genera (Astronium and Schinopsis) are of commercial importance for their timber (Record & Hess 1943). The family is closely related to the Burseraceae and it is not always easy to separate them. In the past they were united as the Therebinthaceae. The genus Thyrsodium was considered by Marchand (1869) as part of the genus Garuga of the Burseraceae.

The summary of the tree species of Anacardiaceae included in this project is given by Table 5.2. below.

Table 5.4. Species of Anacardiaceae studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardium giganteum</td>
<td>16</td>
<td>Zoochory</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Anacardium spruceanum</td>
<td>2</td>
<td></td>
<td>n.o.</td>
</tr>
<tr>
<td>Astronium obliquum</td>
<td>16</td>
<td>Pterochory</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Spondias mombin</td>
<td>1</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Tapirira guianensis</td>
<td>11</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Tapirira peckoltiana</td>
<td>4</td>
<td></td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Tapirira sp. nov.</td>
<td>5</td>
<td></td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Thyrsodium guianense</td>
<td>14</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Thyrsodium spruceanum</td>
<td>6</td>
<td></td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td>Total</td>
<td>75</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Note: C= Cyclic; n.o.= not observed
Anacardium giganteum Hancock ex Engler (code 080)
Vernacular name: Cajú-açu.
Distribution: Northern South America.
Upper storey species of easy identification in the field due to the peculiar large spathulate simple leaves and a watery exudate the thick bark. It was found in four of the eight forest reserves of Jari: São Militão, Angelim, Quaruba and Monte Dourado. A total of 16 individuals were observed, one of which died during the project. Figure 5.1. shows that flowering and fruiting missed the middle year whilst on the third year only one of the individuals flowered and fruited. Fruiting time observed (Figure 5.1) coincided with that reported by Magalhães (1982).

Anacardium spruceanum Bentham (code 082)
Vernacular name: Cajui.
Distribution: Northern South America.
This upper storey species is rarer than its congeneric described above. Only two individuals were observed, neither of which flowered or fruited during the three years of the study. The field appearance of this species is similar to Anacardium giganteum and only a specialist can tell the two apart. According to Magalhães (1982) it sets fruits from September to December.
Astronium obliquum Grisebach (code 050)

Vernacular name: Aroeira.

Distribution: Northern South America.

This upper storey species was studied through 16 individuals occurring in six forests. It can be identified in the field by the typical rectangular-shaped leaflets of its large compound leaves which fall on the ground. The species produce a very hard wood highly valuable commercially. The bark produces small amounts of resin. The wood also produces resin which stains the xylem at a greater or lesser degree, sometimes creating interesting designs on the longitudinally cut wood. Figure 5.2. shows that flowering occurred in the first and third year during August to September. During the first year three out of the 16 individuals flowered and fruited while on the third year only one individual flowered and fruited.

Spondias mombin L. (code 334)

Vernacular name: Taperebá, cajá-mirim, hog plum.

Distribution: Central America and northern South America.

This water-dispersed species occurs mainly in the flooded forests being sporadic in ‘terra firme’ forests. Its presence in these last is probably due to accidental human dispersal while in disturbed areas its occurrence is mainly due to cultivation for the edible fruit. The tree observed in Jari flowered regularly in all the three years of the study, during the last part of the dry season and the onset of the rainy season (December to February). Fruiting was highly extended, occurring in the wet season, from January
to May. This chronology of flowering and fruiting time is consistent with individuals cultivated in Manaus (Prance & da Silva 1975). However flowering and fruiting time in this species is not always the same. In Província de Requena, in Loreto, Perú, this species starts to flower in September, coinciding with the initial rise of the Ucayali river, while fruiting occurs during the flood (Peters and Hammond 1990). Observations in Panama showed that this species flowered in the dry season (March to July) and fruited in the rainy season (July to October) (Croat 1974). The observations of the flowering and fruiting patterns of *Spondias mombin* in tropical America show a great variability between distinct regions. These studies suggest that in *Spondias mombin* flowering and fruiting time is largely controlled by the environment and could be tied to its water dispersed mechanism.

*Tapirira guianensis* Aublet (code 335)

Vernacular name: Tatapiririca.

Distribution: Tropical America.

Eleven individuals of this upper storey species were included in the present study. The species is recognized in the field by the large leaflets of its enormous compound leaves. The graph of Figure 5.3. shows that this species flowered at each of the three years of this study, especially from August to November. Fruiting started in November maturing from February to June.
**Tapirira peckoltiana** Engler (code 310)

Vernacular name: *Tatapiririca peluda*.

Distribution: Northern South America.

Four individuals of this species which occurred at the Jari Ecological Station were studied. In the field this species resembles the former, but its leaflets are thicker and quite hairy. The species flowered from November to February and fruited from February to July (Figure 5.4.).

**Tapirira** sp. nov. (code 307)

Vernacular name: *Tatapiririca vermelha*.

Distribution: Jari river basin.

This upper storey species was represented by five individuals occurring in only one forest. This species is characterized by the large quantity of a thick red resin which occurs in the wood. It flowered from October to January in the first year and from February to April on the third year. Fruiting occurred from November to July (Figure 5.5.).

**Thyrsodium guianense** Sagot, ex March. (code 031)

Vernacular name: Amaparanaré.

Distribution: Central America and northern South America.

This species was represented by 14 individuals. Flowering and fruiteding occurred in all three years of the study (Figure 5.6). Flowering occurred from November to March and fruiteding from February to May.
Thyrsodium spruceanum Bentham (code 030)

Vernacular name: Amaparana.

Distribution: Central America and northern South America.

This species was represented by six individuals. Flowering and fruiting occurred only during the last year of the study (Figure 5.7). Flowering occurred from October to January and fruiting from December to April.

Figure 5.1. Phenology of Anacardium giganteum.
Figure 5.2. Phenology of *Astronium obliquum*.

Figure 5.3. Phenology of *Tapirira guianensis*.
Figure 5.4. Phenology of *Tapirira peckoltiana*.

Figure 5.5. Phenology of *Tapirira* sp. nov.
Figure 5.6. Phenology of *Thyrsodium guianense*.

Figure 5.7. Phenology of *Thyrsodium spruceanum*. 
5.2. BOMBACACEAE

The Bombacaceae is a pantropical family consisting mostly of trees, with 31 genera and 235 species. Of its nine genera only five occur in the neotropics (Robyns 1963). Although Flora Brasiliensis include the genera Bombax and Pachira (Schumann 1886), Robyns monograph (1963) does not recognize the genus Bombax in the neotropics. The species which were formerly placed into Bombax were reclassified by him into Eriotheca and Pseudobombax. The genus Quararibea has been subdivided into two: Quararibea and Matisia by Alverson (1986, 1989). Most neo- and paleotropical Bombacaceae are pollinated by bats.

Table 5.5. Species of Bombacaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bombacopsis nervosa</td>
<td>1</td>
<td>Pogonochory</td>
<td>C. Pluriannual</td>
</tr>
<tr>
<td>Eriotheca crassa</td>
<td>2</td>
<td>&quot;</td>
<td>n.o.</td>
</tr>
<tr>
<td>Eriotheca globosa</td>
<td>3</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Eriotheca surinamensis</td>
<td>8</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Pachira aquatica</td>
<td>2</td>
<td>Hydrochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Pseudobombax munguba</td>
<td>2</td>
<td>Pogonochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Quararibea guianensis</td>
<td>7</td>
<td>Zoolohy</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic

Bombacopsis nervosa (Uittien) A. Robyns (code 549)

Synonym: Bombax nervosum Uittien

Vernacular name: Mamorana da terra firme.

Distribution: Amazon and Guianas, in 'terra firme' forests.

Only one individual of this species was observed, and it flowered and fruited from March to April, but only during the third year of the study.
**Eriotheca crassa** (Uitten) A. Robyns (code 711)

Synonym: *Bombax crassum* Uitten.

Vernacular name: Mamorana.

Distribution: Amazon and Guianas.

Two individuals of this species were observed, neither of which flowered or fruited during the entire length of the study.

---

**Eriotheca globosa** (Aublet) A. Robyns (code 210)

Synonym: *Bombax globosum* Aublet

Vernacular name: Mamorana.

Distribution: Northern South America, from Peru to Brazil’s Maranhão State.

Of the three individuals studied at least one flowered and fruited during the length of the study (Figure 5.8.).

---

**Eriotheca surinamensis** (Uitten) A. Robyns (code 417)

Synonym: *Bombax surinamense* Uitten

Vernacular name: Mamorana da caatinga.

Distribution: Amazon and Guianas, in 'terra firme' forests.

This species was studied by eight individuals in a dry forest, only three of which entered a reproductive stage on the second year of the study (Figure 5.9.). Flowering occurred from August to September while fruiting occurred from October to December. One individual also flowered in January of the first year.
**Pachira aquatica** Aublet (code 623)

Synonym: *Bombax aquaticum* Schumacker

Vernacular name: Mamorana da casca dura.

Distribution: Amazon and Guianas.

Two individuals of this species were observed in the ‘várzea’ forest. Flowering occurred from January to February while fruiting took place from January to April.

**Pseudobombax munguba** (Mart.& Zucc.)Dugand (code 243)

Synonym: *Bombax munguba* Martius

Vernacular name: Munguba.

Distribution: Central America and northern South America.

The two individuals observed flowered from April to August and fruited from July to October, in all three years of the study.

**Quararibea guianensis** Aublet (code 161)

Vernacular name: Inajá-rana.

Distribution: From Costa Rica and Panamá to the Amazon.

This species was studied through seven individuals. Flowering was asynchronous (Figure 5.10).
Figure 5.8. Phenology of *Eriotheca globosa*.

Figure 5.9. Phenology of *Eriotheca surinamensis*. 
Figure 5.10. Phenology of *Quararibea guianensis*.
5.3. BURSERACEAE

The Burseraceae is a pantropical family with 17-20 genera and 600 species. The largest genus, Protium, with some 100 species, is mainly neotropical and it is formed mainly by understorey trees. It is usually dioecious, although many times the flower shows non-functional rudiments of the other sex. The flowers and inflorescence of the Burseraceae may suggest different pollinators for different genera such as Tetrabastris, Trattinickia and Dacryodes. Within species of Protium, however, the flowers and inflorescence do not permit the making of inferences about different pollinators. The fruit of Protium varies in size from 1-3.5 cm, and is considered a dehiscent drupe. The indurate endocarp which serves as a unit of dispersal is called a pyrene or a nucule. The fruit type and phenological characteristics of Protium are indicative of a generalist strategy, geared to a similar range of arboreal or flying dispersal agents, although terrestrial animals may also act as secondary dispersers since fallen pyrenes have been observed to fall on the ground with intact pseudaril. Tetrabastris panamensis is one of the few species of Burseraceae of known disperser, since seeds found in feces of mammals were viable (Daly 1987).
Table 5.6. Species of Burseraceae studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protium alstonii</td>
<td>14</td>
<td>Zoochorous</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium apiculatum</td>
<td>1</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium cuneatum</td>
<td>4</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium decandrum</td>
<td>4</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium giganteum</td>
<td>36</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium guianense</td>
<td>5</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium cf. mori</td>
<td>4</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium nitidifolium</td>
<td>10</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium opacum</td>
<td>21</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium pallidum</td>
<td>9</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium paniculatum</td>
<td>12</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium polybotryum</td>
<td>17</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium robustum</td>
<td>5</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Protium sagotianum</td>
<td>83</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium strumosum</td>
<td>5</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium subserratum</td>
<td>2</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium tenuifolium</td>
<td>8</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium trifoliolatum</td>
<td>2</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium sp. 1</td>
<td>1</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium sp. 2</td>
<td>1</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Protium sp. 3</td>
<td>3</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Tetrastaxis altissima</td>
<td>12</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Tetrastaxis hostmanii</td>
<td>30</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Tetrastaxis panamensis</td>
<td>27</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Trattinickia burseraefolia</td>
<td>6</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Trattinickia glaziovii</td>
<td>1</td>
<td>&quot;</td>
<td>C. Pluriannual</td>
</tr>
<tr>
<td>Total</td>
<td>323</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic

Protium alstonii Sandw. (code 545)

Vernacular name: Breu mescla.

Distribution: Amazon and Guianas.

Of the fourteen individuals observed only four flowered throughout the study of which only one was observed to fruit following flowering. Figure 5.11.

Protium apiculatum Swart vel aff. (code 746)

Vernacular name: Breu vermelho 3.

Distribution: Amazon, Guianas and Costa Rica.
The individual observed flowered in January and February during the first year and in October and November during the third year. Fruiting was observed only on the third year, from December to April.

**Protium cuneatum** Swart (code 454)
Vernacular name: Breu pipiranga.
Distribution: Guianas, Venezuela and lower Amazon.
The type for this species is supposed to be from western Amazonia but the only fertile collections confirmed are from French Guiana and Amapá (Daly 1989 personal communication). In Jari this species occurred only in a population located in the high altitude forests of the Jari Ecological Station (IBAMA) which are similar to the highland forests of the Guianas. Of the four individuals observed only two flowered in December to January of the first year. Fruiting took place from December to July.

Figure 5.12.

**Protium decandrum** (Aublet) Marchand (code 076)
Vernacular name: Breu vermelho.
Distribution: Amazon, French Guiana and Guyana.
Of the four individuals observed three flowered in December to January of the first year, and two trees fruited subsequently, from January to April.

**Protium giganteum** Engler (code 072)
Vernacular name: Breu branco da folha grande.
Distribution: Amazon and Guianas.
36 trees of this species were observed. Flowering and fructing occurred in large peaks during the first year and in a smaller peak during the third year, with no peak observed during the second year. Figure 5.13.

**Protium guianense** (Aublet) Marchand (code 475)
Vernacular name: Breu X.
Distribution: Amazon and Guianas.
Of the five individuals observed only one flowered in January of the third year. This was not followed by fructing.

**Protium cf. mori** Daly (code 630)
Vernacular name: Breu vermelho da folha grande.
Distribution: Eastern Surinam, southern French Guiana and Amapá.
Of the four individuals observed two flowered in December of the first year while three flowered from August to November of the third year, both events were followed by fructing of all trees. Figure 5.14.

**Protium nitidifolium** (Cuatr.) Daly (code 715)
Vernacular name: Breu amaparana.
Distribution: Amazon and Guianas.
Of the ten individuals observed seven flowered from December to February of the first year while two flowered from October to January of the third year. No flowering was observed during the second year whilst fructing was
recorded by only three individuals, during February of the first year. Figure 5.15.

**Protium opacum** Swart cf. subsp. **rabelianum** Daly (code 450)
Vernacular name: Breu jatoá.
Distribution: Amazon and Guianas.
Of the twenty one individuals observed only two flowered during the first year while four flowered during the third year. No flowering was observed during the second year. A peak of fruiting was recorded only during the third year. Figure 5.16.

**Protium pallidum** Cuatr. (code 070)
Vernacular name: Breu branco.
Distribution: Amazon and Guianas.
A peak of flowering occurred during the first and third year, skipping the second year. Fruiting took place only during the first year. Figure 5.17.

**Protium paniculatum** Engler var. **riedelianum** (Engler) Daly (code 257)
Vernacular name: Breu amarelo.
Distribution: Amazon.
A peak of flowering occurred during the first year only although two trees flowered during the third year. Fruiting followed both flowering events. Figure 5.18.

**Protium polybotryum** (Turcz.)Engler subsp. **polybotryum** (code 451)
Vernacular name: Breu vermelho do fruto roxo, breu amescla.
Distribution: Amazon and Guianas.
A peak of flowering occurred during the first and third year, skipping the second year, both followed by fruiting. Figure 5.19.

Protium robustum (Swartz) Poster (code 071)
Vernacular name: Breu folha grande.
Distribution: Amazon and Guianas.
Of the five individuals observed at least three flowered during the first year while two and one flowered during the second and third year respectively. Fruiting occurred mainly during the first year. Figure 5.20.

Protium sagotianum Marchand (code 074)
Distribution: Amazon and Guianas.
Vernacular name: Breu preto.
This species had the largest sample of the present study, with 83 trees observed. It is considered very difficult to separate from Protium tenuifolium (Daly 1989 personal communication). The two species had similar flowering and fruiting phenology. A peak of flowering occurred during the first and third year, missing the second year, both followed by fruiting. Figure 5.21.

Protium strumosum Daly (code 747)
Vernacular name: Breu vermelho do paredão.
Distribution: Amazon.
Of the five individuals observed only two flowered during the first and the third year, followed by fruiting. Figure 5.22.

**Protium subserratum** (Engler) Engler var. (code 579)
Vernacular name: Breu vermelho 2.
Distribution: Amazon and Guianas.
Many matching collections of this species has been placed separately from *Protium subserratum* but no specimen in flower exist to confirm the new species status (Daly 1989 personal communication). Of the two individuals observed, only one flowered during August to September of the third year. No fruiting was observed.

**Protium tenuifolium** Engler (code 453)
Vernacular name: Breu pretense.
Distribution: Central America and northern South America.
The eight individuals observed showed peak flowering during the first and the third year. Fruiting followed but did not show a peak except on the third year. Figure 5.23.

**Protium trifoliolatum** Engler (code 748)
Vernacular name: Breu sem cheiro.
Distribution: Amazon and Guianas.
Of the two individuals observed, only one flowered during January of the first year, followed by fruiting.

**Protium sp. 1** (code 712)
Vernacular name: Breu vermelho 3.
Distribution: Jari.

This tree turned out to be one of three new species of Protium found during the course of this project (Daly 1989 personal communication). The one individual observed only showed fruiting during the first two months of observations.

Protium sp. 2 (code 714)

Vernacular name: Breu folha simples (simple-leaved breu).

Distribution: Jari.

Until the present work only one simple leaved Protium species was known to occur, in the area of Manaus (Daly 1989 personal communication). It is not known whether or not this species is the same until flowering collection is available. The one individual observed only showed flowering during January of the first year of observations.

Protium sp. 3 (code 716)

Vernacular name: Breu amaparana 2.

Distribution: Jari.

Another new species of Protium found during the course of this project, with only three additional collections from elsewhere (Daly 1989 personal communication). Of the three individuals observed two flowered and fruited during the first year of observations, while only one did so during the third year of observations. Figure 5.24.

Tetragastris altissima (Aublet) Swartz (code 073)

Vernacular name: Breu manga.
The 12 trees observed showed a peak of flowering and fruiting during the first and third year, omitting the second year. Figure 5.25.

*Tetragastris* cf. *hostmanii* (Engler) Kuntze (code 452)
Vernacular name: Breu paraense.
Distribution: Amazon and Guianas.
This species was not known to be common in Para, reason for the lack of certainty in the determination (Daly 1989 personal communication). Of the 30 trees observed the largest number to flower at any one year was 8. Flowering and fruiting occurred during all three years of observations. Figure 5.26.

*Tetragastris panamensis* (Engler) O’Kuntze (code 069)
Vernacular name: Breu areu-areu.
Distribution: Central America, Amazon and Guianas.
This species is reported to flower erratically, with heavy crops every 5 or 10 years (R. Foster in Howe 1984). This was not so at Jari where a fixed percentage of individuals flowered and fruited in all three years of the survey. Figure 5.27.

*Trattinickia burseraefolia* Martius (code 455)
Vernacular name: Breu sucuruba branco.
Distribution: Central America, Amazon and Guianas.
Of the six individuals observed one flowered and displayed extended fruiting afterwards. Figure 5.28.
Trattinickia glaziovii Swart (code 749)

Vernacular name: Breu paraense 2.

Distribution: Amazon and Guianas.

The one tree observed flowered from October to December of the third year.
Figure 5.11. Phenology of *Protium altsonii*.

Figure 5.12. Phenology of *Protium cuneatum*.
Figure 5.13. Phenology of *Protium giganteum*.

Figure 5.14. Phenology of *Protium cf. mori*.
Figure 5.15. Phenology of *Protium nitidifolium*.

Figure 5.16. Phenology of *Protium opacum*.
Figure 5.17. Phenology of Protium pallidum.

Figure 5.18. Phenology of Protium paniculatum.
Figure 5.19. Phenology of *Protium polybotryum*.

Figure 5.20. Phenology of *Protium robustum*. 
Figure 5.21. Phenology of *Protium sagotianum*.

Figure 5.22. Phenology of *Protium strumosum*.
Figure 5.23. Phenology of *Protium tenuifolium*.

Figure 5.24. Phenology of *Protium* sp. 3.
Figure 5.25. Phenology of *Tetraastris altissima*.

Figure 5.26. Phenology of *Tetraastris hostmannii*. 
Figure 5.27. Phenology of *Tetragastris panamensis*.

Figure 5.28. Phenology of *Trattinickia burseraefolia*. 
5.4. CARYOCARACEAE

Caryocaraceae is a relatively small family mainly of trees, with about 251 species in two genera. Its distribution ranges from as far north as Costa Rica and as far south as Paraguay, although it is best developed in the Amazon (Lanjouw & Van Heerdt 1941, Record 1943). The most recent monograph of this family is that by Prance and Silva (1973). Several species occur in the Amazon, of which the four species studied occur in the Jari basin. The genus studied, Caryocar, with 17 species of shrubs and medium-sized to very large trees is widely distributed and occur in various habitat types (Prance 1990). The entire genus is thought to be pollinated by bats, while its major seeds predators/dispersers are rodents (Prance 1990). Of the four species studied, Caryocar villosum is a commercial timber in Brazil, used for banister and ship building. The fruit is a source of an edible oil. Both the pulp and the nuts are edible, and it is also attributed medicinal properties (Prance 1990, Pires in prep.).

Table 5.7. Species of Caryocaraceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caryocar alabrum</td>
<td>18</td>
<td>Bar./Zooochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Caryocar microcarpum</td>
<td>5</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Caryocar villosum</td>
<td>3</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Caryocar pallidum</td>
<td>1</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic
*Carvocar glabrum* (Aublet) Pers. (code 284)

Vernacular name: Piquiá-rana.

Distribution: West Indies, tropical South America.

This is the most widespread species of the genus. A peak flowering occurred in all three years of the study. Fruiting however showed a peak only in the first and third years. Figure 5.29.

*Carvocar microcarpum* Ducke (code 285)

Vernacular name: Piquiarana da várzea.

Distribution: Northern South America.

Species adapted to the floodplain forest (Prance 1990). A peak flowering and fruitting occurred in all three years of the study. Figure 5.30.

*Carvocar villosum* (Aublet) Pers. (code 283)

Vernacular name: Piquiá.

Distribution: Northern South America.

Flowering and fruitting occurred irregularly during all three years of the study Figure 5.31.

*Carvocar pallidum* A.C. Smith (code 710)

Vernacular name: Piquiarana 2 (pink stamens)

Distribution: Amazon and Guianas.

The one individual observed flowered during November of the first year and during December of the third year of the study. Fruiting was observed only during the third year.
Figure 5.29. Phenology of *Carvocar glabrum*.

Figure 5.30. Phenology of *Carvocar microcarpum*.
Figure 5.31. Phenology of *Carvocar villosum*.
5.5. CHRYSOBALANACEAE

The Chrysobalanaceae is a medium-sized pantropical family of woody plants containing 17 genera and about 500 species occurring mainly in lowland rainforest (Prance 1989a). The structure of the inflorescence, flower and fruit is very diverse in this family and each genus has unique pollination and dispersal mechanisms (Prance and White 1988). The fruit of the Chrysobalanaceae varies little in its basic structure. It is a drupe with a very large edible seed protected by a hard endocarp. The mesocarp is fleshy and edible or more rarely fibrous and inedible. The fruit is buoyant in some species. The fruit of *Parinari* is a fleshy drupe which may show features associated with particular dispersers. In the genus *Hirtella* the fruit is characteristically small, with a thin juicy mesocarp easily separable from the thin bony endocarp. The fruit of *Licania* is quite variable. Its size ranges from 1.2 cm x 0.8 cm to 10 cm x 5 cm and can be either dry or fleshy. The epicarp can be tomentose, glabrous or verrucous. The thick endocarp can be hard and woody or thin and fibrous. The fruits from some riverine species were seen to be swallowed by fish. The fruit of *Couepia* is 2.5 to 12 cm long or more, with hard granular endocarp. Some species are thought to be dispersed by bats. Distribution data from Prance (1989a).
Table 5.8. Species of *Chrysobalanaceae* studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Couepia guianensis</td>
<td>8</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Couepia joaquinae</td>
<td>4</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Couepia robusta</td>
<td>1</td>
<td>&quot;</td>
<td>n.o.</td>
</tr>
<tr>
<td>Hirtella bicornis</td>
<td>35</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Hirtella eriandra</td>
<td>4</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Hirtella obidensis</td>
<td>9</td>
<td>&quot;</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Hirtella piresii</td>
<td>9</td>
<td>&quot;</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Licania apetala</td>
<td>4</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Licania canescens</td>
<td>4</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania egleri</td>
<td>15</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania heteromorpha</td>
<td>32</td>
<td>&quot;</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Licania impressa</td>
<td>4</td>
<td>&quot;</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Licania kunthiana</td>
<td>8</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania laevigata</td>
<td>9</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Licania latifolia</td>
<td>3</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Licania macrophylla</td>
<td>8</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania micrantha</td>
<td>12</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Licania minutiflora</td>
<td>2</td>
<td>&quot;</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Licania octandra</td>
<td>6</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania pallida</td>
<td>13</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Licania robusta</td>
<td>4</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Licania silvae</td>
<td>2</td>
<td>&quot;</td>
<td>n.o.</td>
</tr>
<tr>
<td>Parinari excelsa</td>
<td>17</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>213</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic; A = Acyclic

*Couepia guianensis* Aublet sub. sp. *divaricata* (Huber) Prance (code 131)

Vernacular name: Cumatê.

Distribution: Amazon and Guianas.

Of the eight individuals observed the maximum number seen in flower was two, during the second year. Flowering occurred irregularly during the three years of the study, although mostly during the dry season. Fruiting followed closely the flowering pattern and was highly extended. Figure 5.32.
**Couepia joaquiniae** Prance (code 414)

Vernacular name: Cumatê 2.

Distribution: Jari river basin, in Amapá.

This species flowered during the first and third years of the study, followed by fruiting. The ripe fruits have a bright yellow colour and are either consumed by animals or let to rot under the tree until only the fibrous woody endocarp remains. Figure 5.33.

**Couepia robusta** Huber (code 252)

Vernacular name: Pajurá.

Distribution: Amazon.

The individual observed did not flower or fruit during the entire length of the study.

**Hirtella bicorns** Mart. & Zucc. (code 158)

Vernacular name: Farinha seca branca.

Distribution: Tropical South America.

Although a large number of trees were observed (35), the average number of trees that flowered was very small, except during the third year of the study. A peak flowering can be easily detected during the dry season, while a peak fruiting can also be detected slightly shifted to the left. Figure 5.34.

**Hirtella eriandra** Bentham (code 700)

Vernacular name: Farinha seca vermelha 2.

Distribution: Northern South America.
A peak flowering can be easily detected during the dry season, while a peak fruiting can also be detected slightly shifted to the left. Figure 5.35.

**Hirtella obidensis** Ducke (code 462)
Vernacular name: Caripê vermelho.
Distribution: Lower Amazon and Guianas.
Of the nine individuals observed only one flowered and fruited during the first two years of observations. During the third year a total of eight individuals flowered and fruited. Figure 5.36.

**Hirtella piresii** Prance (code 144)
Vernacular name: Farinha seca vermelha.
Distribution: Lower Amazon and Guianas.
Of the nine individuals observed only one flowered and fruited during the first year of observations. No flowering or fruiting was observed during the second year, but a total of eight individuals flowered and fruited during the third year. Figure 5.37.

**Licania apetala** (E.Mey.) Fritsch (code 550)
Vernacular name: Caripê da várzea, caripê matupiri.
Distribution: Tropical South America.
Flowering occurred during the end of the dry season (October to December), while fruiting occurred during the beginning of the rainy season (January). Figure 5.38.
**Licania canescens** R. Ben. (code 701)

Vernacular name: Caripê branco 2.

Distribution: Amazon, Guianas and Bahia.

This species flowered irregularly during the first and third years of the study, followed by fruiting. Figure 5.39.

**Licania egléri** Prance (code 702)

Vernacular name: Caripê matupiri 2.

Distribution: Amazon.

This species has sweet scented flowers which are visited by innumerable small bees of the genera *Apis* and *Trigona* (Prance & White 1988). Of the 15 individuals observed only one flowered and fruited during the first two years of observation. During the third year of observation up to nine individuals were observed in flower. The flowering of this species can be considered highly irregular. Figure 5.40.

**Licania heteromorpha** Bentham (code 206)

Vernacular name: Macucú.

Distribution: Amazon, Guianas and eastern Brazil.

This is the commonest and the most collected Amazon species of *Licania* with five recognized varieties (Prance 1989). 32 individuals of this species were observed. Flowering and fruiting was extended and highly irregular. Figure 5.41.

**Licania impressa** Prance (code 385)

Vernacular name: Caripê branco.
Distribution: Middle and lower Amazon.
Of the four trees observed three showed a peak fruiting during the first part of the rainy season of the first year studied. Flowering was observed during March and April of the third year studied. Figure 5.42.

Licania kunthiana Hook. f. (code 089)
Vernacular name: Caripê pintadinho.
Distribution: Tropical South America.
Flowering occurred mainly during the end of the dry season but also occurred during the end of the wet season. Fruiting followed the irregular pattern of flowering, with much year to year variation. Figure 5.43.

Licania laevigata Prance (code 704)
Vernacular name: Macucu vermelho 2.
Distribution: Central to lower Amazon, Suriname.
Of the nine individuals studied only two were observed to flower for a very brief time, while only one fruited from August to September, all during the third year of the study. Figure 5.44.

Licania latifolia Benth. ex Hook. (code 508)
Vernacular name: Macucú vermelho.
Distribution: Amazon and Surinam
This species showed some flowering towards the end of the dry season, and extended fruiting during the wet season. Figure 5.45.
Licaniia macrophylla Bentham (code 085)
Vernacular name: Macucú branco, anoerá.
Distribution: Amazon and Guianas.
Eight individuals of this species were observed whose flowering and fruiting was extended and highly irregular. Figure 5.46.

Licaniia micrantha Miq. (code 464)
Vernacular name: Caripê-rana amarela.
Distribution: Northern South America and eastern Brazil.
12 individuals of this species were observed whose flowering and fruiting was extended and highly irregular. Figure 5.47.

Licaniia minutiflora (Sagot) Fritsch (code 591)
Vernacular name: Pajurá da várzea
Distribution: Amazon and Guianas.
Only two individuals of this species were studied. Flowering and fruiting was highly extended. During the first two years flowering occurred from October to February, while fruiting followed the same pattern.

Licaniia octandra (Hoff. ex R.& S.) Kuntze (code 034)
Vernacular name: Caripê seco.
Distribution: Tropical South America.
Six individuals of this species were studied. Flowering and fruiting was highly extended and irregular. Figure 5.48.
**Licania pallida** Spruce ex Sagot (code 463)
Vernacular name: Caripê pintadinho 2.
Distribution: Amazon.

13 individuals of this species were studied. Flowering and fruiting were highly extended and irregular, with the first occurring mainly during the dry and the second during the wet season. Figure 5.49.

**Licania robusta** Sagot (code 090)
Vernacular name: Cariperana amarela 2.
Distribution: Amazon and Guianas.

Four individuals of this species were studied. Flowering and fruiting was highly irregular. Figure 5.50.

**Licania silvae** Prance (code 709)
Vernacular name: Farinha seca vermelha 3.
Distribution: Amazon.

Only two individuals of this species were studied, neither of which flowered or fruited throughout the study.

**Parinari excelsa** Sabine (code 258)
Vernacular name: Parinari.
Distribution: Northern South America, eastern Brazil.

This is the mostly widespread species of the genus, extending from Colombia to southeast Brazil and occurring also in Africa. 17 individuals of this species were studied. Flowering and fruiting were highly extended and irregular. Figure 5.51.
Figure 5.32. Phenology of *Couepia guianensis*.

Figure 5.33. Phenology of *Couepia joaquinae*. 

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Figure 5.34. Phenology of *Hirtella bicornis*.

Figure 5.35. Phenology of *Hirtella eriandra*.
Figure 5.36. Phenology of *Hirtella obidensis*.

Figure 5.37. Phenology of *Hirtella piresii*.
Figure 5.38. Phenology of *Licania apetala*.

Figure 5.39. Phenology of *Licania canescens*.
Figure 5.40. Phenology of *Licania egleri*.

Figure 5.41. Phenology of *Licania heteromorpha*. 
Figure 5.42. Phenology of *Licania impressa*.

Figure 5.43. Phenology of *Licania kunthiana*.
Figure 5.44. Phenology of *Licania laevigata*.

Figure 5.45. Phenology of *Licania latifolia*. 
Figure 5.46. Phenology of *Licania macrophylla*.

Figure 5.47. Phenology of *Licania micrantha*.
Figure 5.48. Phenology of *Licania octandra*.

Figure 5.49. Phenology of *Licania pallida*.
Figure 5.50. Phenology of *Licania robusta*.

Figure 5.51. Phenology of *Parinari excelsa*.
5.6. CONNARACEAE

The Connaraceae is a small pantropical family of woody plants with 16 genera and 300-350 species. In the neotropics it is represented by five genera and 101 species ranging from Mexico and Cuba to southern Brazil (Forero 1983). The genus studied, Con narus has only one tree species in the Jari basin.

Table 5.9. Species of Connaraceae studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number Individuals</th>
<th>Diaspore Type</th>
<th>Phenology Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>Con narus derrotteii</td>
<td>9</td>
<td>Zoochory</td>
<td>A. Massive-Ext.</td>
</tr>
</tbody>
</table>

Note: A = Acyclic

Con narus derrotteii (DC.) Planchon var. angustifolius Radlkofer (code 239)

Synonym: Con narus angustifolius (Radlkofer) Schellenberg

Vernacular name: Muirassacaca.

Distribution: Central America, northern South America.

This subspecies occurs in Amapá, Amazonas, Mato Grosso, Pará and Guianas. Nine individuals of this species were observed, all occurring in the two savanna forests studied. The year-long irregular flowering pattern mentioned by Forero (1983) was confirmed by the observations of this study (Figure 5.52).
Figure 5.52. Phenology of *Connarus perrottettii*.
5.7. HUMIRIACEAE

The Humiriaceae is a small pantropical family of trees or shrubs occurring mainly in the neotropics. It has 4 genera (Humiria, Saccoglottis, Endopleura and Vantanea) and some 30 species. The fruit is drupaceous with few stones and the seeds have fleshy albumen (Brink 1941, Cuatrecasas 1961).

Table 5.10. Species of Humiriaceae studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endopleura uchi</td>
<td>19</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Humiria balsamifera</td>
<td>15</td>
<td>Endozoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Saccoglottis guianensis</td>
<td>27</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Vantanea parviflora</td>
<td>26</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Total</td>
<td>87</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic

Endopleura uchi (Huber)Cuatr. (code 348)

Synonym: Sacoglottis uchi Huber.

Vernacular name: Uchi.

Distribution: Central and lower Amazon.

The fruit of this species is an ellipsoid greenish-yellow drupe, 4-6 cm x 2-3.8 cm, with a thin edible mesocarp (2.5 mm). Flowering occurred mostly during the dry season while fruiting extended itself from the dry into the wet season. Figure 5.53.

Humiria balsamifera (Aublet)J. St. Hil. (code 359)

Vernacular name: Umiri.

Distribution: Tropical America.
Flowering occurred mostly during the dry season while fruiting occurred also at the end of the dry season. Figure 5.54.

*Saccoglottis guianensis* Benth. (code 349)
Vernacular name: Uchirana.
Distribution: Amazon and Guianas.
Flowering occurred mostly during the dry season while fruiting occurred during the beginning of the wet season.
Flowering and fruiting highly extended. Figure 5.55.

*Vantanea parviflora* Aublet (code 259)
Vernacular name: Parurú.
Distribution: Amazon and Guianas.
Flowering and fruiting were irregular and highly extended.
Figure 5.56.
Figure 5.53. Phenology of *Endopleura uchi*.

Figure 5.54. Phenology of *Humiria balsamifera*.
Figure 5.55. Phenology of *Saccoglottis guianensis*.

Figure 5.56. Phenology of *Vantanea parviflora*.
5.8. LECYTHIDACEAE

The Lecythidaceae is a pantropical family of small to very large trees and shrubs with 17 genera and about 140 species (Eyra 1934). They grow mainly in undisturbed moist forests with only a few species adapted to savanna vegetation (Mori & Prance 1987a,b). Taxonomically the family is subdivided into three subfamilies. Most of the neotropical Lecythidaceae belong to the subfamily Lecythidoideae, with 200 species and ten genera. Most Lecythidaceae are thought to be allogamous plants (Prance 1976). They have flowers with specialized structures to attract and accommodate specialized pollinators, such as a stamen ring and flower hood (Prance 1976, Prance & Mori 1979, Mori & Prance 1987b, 1990). Asexual reproduction has been reported for this family, with sprouting noted for Lecythis alba, Gustavia superba (Prance & Mori 1979) and Bertholletia excelsa (personal note).

The phenology of Lecythidaceae has been studied by Prance and Mori (1979) and by Mori and Prance (1987a). Prance and Mori (1979) analyzed several years of phenology data of various Lecythidaceae trees occurring in the 'Reserva Florestal Ducke' of the 'Instituto Nacional de Pesquisas da Amazônia (INPA). They pointed out that not all individuals entered the flowering stage every year. For instance, one tree of Lecythis that was observed during ten years flowered in only five years, while another that was observed for five years flowered in only three. Based on
this and other observational studies Prance and Mori (1979) devised three types of strategies according to the sequence of leaf drop, flushing and flowering. Another finding was the different flowering times observed for several closely related sympatric species of Lecythidaceae. The second study, by Mori and Prance (1987a), was carried out in French Guiana, and describes in detail the various flowering modes of each species. It found no phenological separation between the various Eschweilera studied including two species that are very similar. With exception of one ‘varzea’ species of Eschweilera all the species flowered during the dry season and beginning of the wet season. The most common pollinators of Lecythidaceae are bees except for one species - Lecythis poiteaui Berg - known to be pollinated by bats (Mori & Prance 1987a). They have also evolved a variety of fruit forms which suggest a parallel with dispersers and/or predators. Flowering and fruiting phenology of Gustavia superba in Panama was described by Mori and Kallunki (1976) and Prance and Mori (1979).
Table 5.11. Species of Lecythidaceae studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bertholletia excelsa</td>
<td>22</td>
<td>Sinzoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Couratari guianensis</td>
<td>12</td>
<td>Pterochory</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Couratari oblongifolia</td>
<td>1</td>
<td></td>
<td>A. Rare</td>
</tr>
<tr>
<td>Couroupita guianensis</td>
<td>2</td>
<td>Zoochory</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Eschweilera amazonica</td>
<td>9</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Eschweilera coriacea</td>
<td>25</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Eschweilera grandiflora</td>
<td>1</td>
<td></td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td>Eschweilera obversa</td>
<td>8</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Eschweilera pedicellata</td>
<td>9</td>
<td></td>
<td>C. Annual</td>
</tr>
<tr>
<td>Eschweilera sp. l</td>
<td>10</td>
<td></td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Gustavia augusta</td>
<td>24</td>
<td>Atelechory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Gustavia hexapetala</td>
<td>1</td>
<td></td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td>Lecythis corrugata</td>
<td>4</td>
<td></td>
<td>A. Rare</td>
</tr>
<tr>
<td>Lecythis idatimon</td>
<td>4</td>
<td></td>
<td>A. Rare</td>
</tr>
<tr>
<td>Lecythis lurida</td>
<td>11</td>
<td></td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Total</td>
<td>143</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic; A= Acyclic

Bertholletia excelsa Humb. & Bonpl. (code 097)

Vernacular name: Castanha do Pará, brazil nut tree.

Distribution: Amazon and Guianas.

Due to its importance this is one of the most studied species of Amazonian trees. A comprehensive review of its biology is given by Mori and Prance (1990). Its flowering and fruiting phenology were studied by various researchers of the ‘Centro de Pesquisa Agropecuária do Trópico Húmido’ (EMBRAPA/CPATU), in Belém (Müller et al. 1980, Müller 1981, Moritz 1984). Flowering was found to be very regular on a year to year basis, occurring from the end of the dry season to the start of the rainy season but peaking around January or February. The fruit is a round woody pixidium, 14 cm diameter, with a 8 mm operculum in the apex, inside which are some 20-30 nuts. Fruiting also displayed regularity and a curve similar to flowering only shifted.
towards the right. The fruit maturation takes 15-18 months to complete. Only full sized fruits were recorded for phenology, so the fruiting curves seen refers to the previous year’s flowering. Figure 5.57.

**Couratari guianensis** Aublet (code 338)

Vernacular name: Tauarí.

Distribution: Amazon and Guianas.

Of the 12 individuals observed none flowered or fruited throughout the study.

**Couratari oblongifolia** Ducke & Knuth (code 535)

Vernacular name: Tauari branco.

Distribution: Amazon and Guianas.

Only one individual was observed and it did not flower or fruit.

**Couroupita guianensis** Aublet (code 095)

Vernacular name: Castanha de macaco, cannon ball tree.

Distribution: Central America and northern South America.

This species has large, round indehiscent fruits, whose seeds are eaten by monkeys. Only two individuals were observed. Flowering and fruiting were irregular between different years. Figure 5.58.

**Eschweilera amazonica** R. Knuth (code 230)

Vernacular name: Matá matá ‘c’.

Distribution: Amazon and Guianas.
Flowering and fruiting irregular. During year two there was a peak flowering during the first part of the wet season, followed by a peak in fruiting. Figure 5.59.

**Eschweilera coriacea** (A.P. DC.)Mart. ex Berg (code 227)

Vernacular name: Matá matá branco.
Distribution: Amazon and Guianas.

In this species flowering was consistent in the middle of the dry season (November), while fruiting occurred mostly during the first part of the wet season. No fruiting was observed during the second year of the study. Figure 5.60.

**Eschweilera grandiflora** (Aublet) Sandwith (code 407)

Vernacular name: Matá-matá da flor grande
Distribution: Amazon and Guianas.

This species is thought to retain its flowers for several days. The only individual observed flowered only once, during January to February of the first year of the study.

**Eschweilera obversa** (Berg) Miers (code 228)

Vernacular name: Matá matá castanhola.
Distribution: Amazon and Guianas.

Flowering was irregular, with peaks in either the wet or the dry season. Fruiting also occurred irregularly. Figure 5.61.

**Eschweilera pedicellata** (Richard) Mori (code 208)

Vernacular name: Matá matá rosa da terra firme
Distribution: Amazon and Guianas.
This species is thought to retain its flowers for several days. Flowering and fruiting regular although only one individual flowered during the second year of the study. Flowering occurred on a peak coinciding with the end of the dry season, while fruiting always occurred during the wet season. Figure 5.62.

*Eschweilera* sp. 1 (code 718)
Vernacular name: Mata mata branco do paredão.
Distribution: Jari river basin.
Flowering missed the middle year. When it occurred it did so at the end of the dry season or at the beginning of the wet season. Fruiting took place during the wet season. Figure 5.63.

*Gustavia augusta* L. (code 153)
Vernacular name: Geniparana
Distribution: Northern South America.
Mori et al. (1978) reported that this species opens its flowers at night and retains the petals and androecium until late on the following afternoon. The fruits have indehiscent pericarps and the seeds are released only when the pericarp rots. Most fruits found in the forest floor at Jari were full of germinated seeds. Flowering and fruiting both occurred as peaks at the end of the dry season or beginning of the rainy season. There was also at least one individual flowering and fruiting at irregular times. Figure 5.64.
**Gustavia hexapetala** (Aublet) J.E. Smith (code 178)

Vernacular name: Jarana, geniparana da várzea.

Distribution: Amazon and Guianas.

One individual was observed and it flowered once during the three year study, from April to June, and fruited in an extended way, from July to February. This wet season flowering pattern was also found for the same species growing in a seasonal forest in French Guiana (Prance 1976, Mori & Prance 1987a).

**Lecythis corrugata** Poiteau subsp. **corrugata** (code 181)

Vernacular name: Jateréu morrão.

Distribution: Amazon and Guianas.

Although this species is considered typical of savanna forests (Prance & Mori 1979) in Jari the trees were found in a mesophytic forest rather than in the two savanna forests studied. Only one of the four individuals observed flowered, doing so in July and then from December to February. No fruiting was observed. Figure 5.65.

**Lecythis idatimon** Aubl. (code 229)

Vernacular name: Jateréu.

Distribution: Amazon and Guianas.

Out of the four individuals observed one flowered from February to March and fruited from March through May. Figure 5.66.
Lecythis lurida (Miers) Mori (code 497)

Vernacular name: Matá-matá jarana.

Distribution: Amazon and Guianas.

Eleven individuals were observed. Flowering was highly extended, from the end of the dry season to the first part of the rainy season. Fruiting occurred during the transition from dry to wet season and also during the wet season. Figure 5.67.

![Graph showing phenology of Bertholletia excelsa over years 1987 to 1990. Index of month ranges from 1 to 6.](image)

**Figure 5.57. Phenology of Bertholletia excelsa.**
Figure 5.58. Phenology of *Couroupita guianensis*.

Figure 5.59. Phenology of *Eschweilera amazonica*. 
Figure 5.60. Phenology of *Eschweilera coriacea*.

Figure 5.61. Phenology of *Eschweilera obversa*. 

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Figure 5.62. Phenology of *Eschweilera pedicellata*.

Figure 5.63. Phenology of *Eschweilera* sp. 1.
Figure 5.64. Phenology of *Gustavia augusta*.

Figure 5.65. Phenology of *Lecythis corrugata*.
Figure 5.66. Phenology of *Lecythis idatimon*.

Figure 5.67. Phenology of *Lecythis lurida*.
The Leguminosae or Fabaceae is a large cosmopolitan family of herbaceous to woody plants. It has about 670 genera and 18,000 species subdivided into three subfamilies: Cesalpinioideae, Papilionoideae and Mimosoideae. It is probably the largest and most important plant family in the Amazon. Due to the large number of leguminous tree species occurring at Jari (132), only the subfamily Mimosoideae was included in the present study. This subfamily has 49 species of trees at the Jari river basin alone. From this group the most common and easily identifiable species were selected as well as some species of Inga, a difficult genus which had been studied by Poncy (1985) in French Guiana. A study by Koptur (1984) on several Inga species at Costa Rica revealed that they were all allogamous and that intraspecific crosspollination in several species was more successful when the pollen source was more than one Km away from the stigmatic parent than when pollen source was less than 0.5 Km away.

*Cedrelinga cateniiformis* (Ducke) Ducke (code 107)

Vernacular name: Cedrorana, iacaiaca.

Distribution: Surinam, Amazonian Brazil, Peru and Ecuador. Flowering and fruiting skipped the middle year (88-89). Flowering occurred at the end of the dry season and beginning of the rainy season. Fruiting occurred from March to June. Figure 5.68.
Table 5.12. Species of *Leguminosae - Mimosoideae* studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cedrelina cateniiformis</em></td>
<td>14</td>
<td>Ciclochory</td>
<td>C. Biennial</td>
</tr>
<tr>
<td><em>Dinizia excelsa</em></td>
<td>31</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Inga acrocephala</em></td>
<td>2</td>
<td>Endozoochory</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td><em>Inga alba</em></td>
<td>33</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td><em>Inga capitata</em></td>
<td>2</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Inga edulis</em></td>
<td>3</td>
<td>&quot;</td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td><em>Inga cf. negrensis</em></td>
<td>1</td>
<td>&quot;</td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td><em>Inga cf. panurensis</em></td>
<td>1</td>
<td>&quot;</td>
<td>C. Pluriann.</td>
</tr>
<tr>
<td><em>Inga paraensis</em></td>
<td>1</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Inga pezizifera</em></td>
<td>2</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Inga rubiginosa</em></td>
<td>19</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td><em>Inga thibaudiana</em></td>
<td>11</td>
<td>&quot;</td>
<td>A. Massive</td>
</tr>
<tr>
<td><em>Inga sp.</em></td>
<td>3</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Marraoxylon racemosum</em></td>
<td>37</td>
<td>Pogonochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Parkia decussata</em></td>
<td>1</td>
<td>Zoochory</td>
<td>A. Rare</td>
</tr>
<tr>
<td><em>Parkia oppositifolia</em></td>
<td>22</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td><em>Parkia ulei</em></td>
<td>14</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td><em>Pentaclethra macroloba</em></td>
<td>24</td>
<td>Barochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td><em>Piptadenia communis</em></td>
<td>47</td>
<td>Ciclochory</td>
<td>A. Rare</td>
</tr>
<tr>
<td><em>Zygia ampla</em></td>
<td>7</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>275</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic; A = Acyclic

*Dinizia excelsa* Ducke (code 038)

Vernacular name: Angelim vermelho.

Distribution: Amazon and Guianas

Flowering varied from year to year in the present study. During the first year it occurred from May to September. During the second year from July to December and during the third year from August to December. Fruiting was extended and may take up to 12 months to complete. The mature fruits fall at the end of the dry season at the same time that young ones are appearing. Figure 5.69.
**Inga acrocephala** Steud. (code 624)

Vernacular name: Ingá.
Distribution: Amazon and Guianas.

Only two individuals were observed. One of them flowered in August of the first year and fruited from June to July of the second year. The other showed fruits in May and again flowers in July, of the second year.

**Inga alba** (Sw.) Willd. (code 167)

Vernacular name: Ingá xixi.
Distribution: Amazon and Guianas.

This species had a very irregular pattern of flowering and fruiting. Figure 5.70.

**Inga capitata** Desv. (code 480)

Vernacular name: Ingá.
Distribution: Amazon and Guianas, Bahia (Brazil).

Two individuals was observed, both of which died during the third year of the study. They fruited from March to May of the first year. Then they flowered in July of the second year.

**Inga edulis** Martius (code 163)

Vernacular name: Ingá cipó.
Distribution: Tropical America.

Only three individuals were observed. They flowered from August to September of the third year only, fruited from October to November. Figure 5.71.
*Inga cf. negrensis* Bentham (code 641)
Vernacular name: Ingá amarelo.
Distribution: Amazon and Guianas.
Only one individual was observed. It flowered from October to January and fruited from February to March, but only during the third year of the study.

*Inga cf. panurensis* Spruce ex Bentham (code 642)
Vernacular name: Ingá.
Distribution: Amazon and Guianas.
Only one individual was observed. It fruited from June to July, but only during the second year of the study.

*Inga paraensis* Ducke (code 388)
Vernacular name: Ingá vermelho.
Distribution: Amazon and Guianas.
Only one individual was observed. It flowered in August of the second year of the study. It fruited in May, during the first year of the study.

*Inga pezizifera* Bentham (code 165)
Vernacular name: Ingá grande.
Distribution: Central America, Amazon and Guianas.
Only two individuals were observed, one of which flowered in March of the second and third years of the study and fruited in April.
**Inga rubiginosa** (Rich.) DC. (code 166)

Vernacular name: Ingá peludo.

Distribution: Amazon and Guianas.

The 19 individuals observed showed irregular flowering with a peaked in August. Fruiting was also irregular and showed peaks from April to May. Figure 5.72.

**Inga thibaudiana** DC. (code 640)

Vernacular name: Ingá cipo 2.

Distribution: Central America and tropical South America.

Flowering and fruiting very irregular, although flowering showed peaks in July. Figure 5.73.

**Inga sp.** (code 644)

Vernacular name: Ingá.

Distribution: Jari river basin.

Out of the three individuals observed only one flowered and fruited. Flowering occurred from June to September and fruiting occurred from October to December. Figure 5.74.

**Marmaroxyylon racemosum** (Ducke) Killip (code 041)

Vernacular name: Angelim rajado.

Distribution: Amazon.

This species flowers during the end of the dry season and beginning of the wet season. Fruiting occurs during the wet season. Figure 5.75.
Parkia decussata Ducke (code 376)
Vernacular name: Fava arara tucupi.
Distribution: Amazon and French Guiana.
Only one individual was observed and it did not flower or fruit throughout the study.

Parkia oppositifolia Bentham (code 126)
Synonym: Parkia nitida Miq.
Vernacular name: Fava coré.
Distribution: Southern Panama, Venezuela, Amazon and Guianas.
Flowering occurred from February to May, that is, during the wet season. Fruiting was extended and occurred only during the first year of the study. Figure 5.76.

Parkia ulei (Harms) Kuhlm. var. surinamensis (code 143)
Vernacular name: Esponjeira.
Distribution: Eastern Amazonian Brazil, NE Venezuela and Guianas.
Flowering occurred from February to June during the first year of the study, then August-September during the second year and finally April to August during the third year of the study. Fruiting was extended and variable. Figure 5.77.

Pentaclethra macroloba (Willd.) Kuntze
Vernacular name: Pracaxi.
Distribution: Tropical America and Africa.
This common, easily identifiable species has been the subject of several ecological studies such as Hazlett 1987.
It is considered a typical 'várzea' species but it extends to dense 'terra firme' forests in areas of abundant rainfall (Hazlett 1987). It flowers during the dry season (August - December). Fruiting is extensive, starting at the end of the dry season and extending throughout the wet season. Figure 5.78.

**Piptadenia communis** Bentham (code 343)

Vernacular name: Timborana.

Distribution: Amazonian Brazil and Guianas.

Although 47 individuals were observed, only two were seen to flower at any one time and only four were observed in fruit. Flowering and fruiting were very irregular, with mature fruits occurring mainly during the wet season. Figure 5.79.

**Zygia ampla** (Spruce ex Bentham) Pittier (code 616)

Vernacular name: Jarandeua.

Distribution: Amazonian Brazil and Guianas.

Seven individuals were observed. They flowered from April to July, but only during the second year of the study. No fruiting was observed.
Figure 5.68. Phenology of *Cadrelinga cateniiformis*.

Figure 5.69. Phenology of *Dinizia excelsa*. 
Figure 5.70. Phenology of *Inga alba*.

Figure 5.71. Phenology of *Inga edulis*.
Figure 5.72. Phenology of *Inga rubiginosa*.

Figure 5.73. Phenology of *Inga thibaudiana*. 
Figure 5.74. Phenology of *Inea* sp.

Figure 5.75. Phenology of *Marmaroxylon racemosum*.
Figure 5.76. Phenology of *Parkia oppositifolia*.

Figure 5.77. Phenology of *Parkia ulei*.
Figure 5.78. Phenology of *Pentaclethra macroloba*.

Figure 5.79. Phenology of *Piptadenia communis*.
5.10. MELIACEAE

The family Meliaceae is one of the most important sources of tropical timbers such as the renowned mahogany and the South American cedar. It is a large pantropical family of trees or treelets, rarely shrubs. The entire family has 580 species and in the neotropics ten genera and 120 species are recognized, occurring from Costa Rica to southeastern Brazil (Pennington et al. 1981). A large number of species of the Meliaceae were found to have unisexual flowers monoecious or dioecious. Sexual dimorphism is widespread within the family. The fruit is a loculicidal or septifragal capsule or rarely a drupe. The fruits of Guarea are conspicuous capsules adapted to attract dispersers. The fruits of Trichilia are uniform in relation to pericarp structure but vary considerably with respect to the arillode which surrounds the seeds. The seed is either winged and then usually attached to a large woody columella or unwinged and then usually with a fleshy arillode or sarcotesta (Pennington et al. 1981).

Existing phenological information on the species of this family was reviewed by Pennington et al. (1981). He called attention for the fact that many species of this family are able to flower at very early stage. The flowering and the phenology of the dioecious Guarea rhopalocarpa was studied by Bullock et al. (1982) in Costa Rica. This study revealed no tendency by either sex to
differ in the number of flowering episodes per year (Bullock et al. 1982).

Table 5.13. Species of Meliaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carapa guianensis</td>
<td>32</td>
<td>Hydrochory</td>
<td>A. Massive-Ext.</td>
</tr>
<tr>
<td>Cedrela odorata</td>
<td>2</td>
<td>Pterochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Guarea kunthiana</td>
<td>11</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Guarea macrophylla</td>
<td>6</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Guarea pubescens</td>
<td>2</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Guarea purusana</td>
<td>6</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Trichilia cf. hirta</td>
<td>2</td>
<td>&quot;</td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Trichilia lecoitei</td>
<td>2</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Trichilia micrantha</td>
<td>1</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Trichilia quadrijuga</td>
<td>1</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Trichilia schomburkii</td>
<td>2</td>
<td>&quot;</td>
<td>C. Pluriannual</td>
</tr>
<tr>
<td>Trichilia septentrionalis</td>
<td>3</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Total</td>
<td>70</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic; A = Acyclic

**Carapa guianensis** Aubl. (code 035)

Vernacular name: Andiroba.

Distribution: Tropical America.

Monoecious species with unisexual flowers but these with well developed vestiges of the opposite sex. The fruit is a large, pendulous subwoody, subglobose septifragal capsule. Each capsule has 8-35 large angular seeds. Cotyledons large and fused. Flowering and fruiting occurred every year on an extended manner. Figure 5.80.

**Cedrela odorata** L. (code 106)

Vernacular name: Cedro vermelho.

Distribution: Central and South America.

Monecious species. The fruit is an oblong-ellipsoid to obovoid 5-valved capsule with dry winged seeds. Only two individuals were observed. Flowering must take place very
quickly since it was not observed during our monthly visits. Fruiting occurred from June to October or even December.

**Guarea kunthiana** A. Juss. (code 489)
Vernacular name: Jatoá vermelho.
Distribution: Central America to Paraguay.
Dioecious plants. Flowering was observed from September to February. Fruiting is extended, starting at the end of the dry season and ending during the wet season. Figure 5.81.

**Guarea macrophylla** Vahl (code 724)
Vernacular name: Jataúba vermelha 2.
Distribution: Tropical America, from the Caribbean islands to Paraguai. Flowering must take place very quickly since it was not observed during our monthly visits. Fruiting occurred from February to August, but only during the second year of the study. Figure 5.82.

**Guarea pubescens** (Rich.) A. Juss. (code 725)
Vernacular name: Jataúba peluda.
Distribution: Amazon and Guianas.
Plants dioecious or hermaphrodite. Flowering must take place very quickly since it was not observed during our monthly visits. Fruiting occurred from April to July.

**Guarea purusana** C. DC. (code 731)
Vernacular name: Jatoá vermelho da várzea.
Distribution: Amazon.
Flowering and fruiting highly irregular. Figure 5.83.

**Trichilia cf. hirta** (code 726)

Vernacular name: Jataúba vermelha 2.

Distribution: Central America, western Amazon, southeastern Brazil and Paraguay.

Dioecious plants. Only two individuals were observed. It is reported to flower at least once a year (Pennington et al. 1981). In Jari flowering was observed in October and January of the first year of the study and then from October to December of the second year.

**Trichilia lecointei** Ducke (code 569)

Vernacular name: Jataúba branca.

Distribution: Lower Amazon and Guianas.

Only two individuals were observed. Fruiting was observed in September of the first year of the study.

**Trichilia micrantha** Bentham (code 727)

Vernacular name: Jataúba branca 2.

Distribution: Amazon and Guianas.

Species monoecious, dioecious and hermaphrodite. Only one individual was observed. It flowered from April to July of the second year of the study. No fruiting was observed.

**Trichilia quadrijuga** Kunth (code 728)

Vernacular name: Jataúba branca 3.

Distribution: Central America to eastern Brazil (Bahia).
Only one individual was observed. In Jari it did not flower or fruit throughout the study.

**Trichilia schomburgkii** C. DC. (code 729)

Vernacular name: Jataúba vermelha 3.

Distribution: Northern part of South America.

Dioecious plants. Out of the two individuals observed one flowered from February to March and fruited in April of the third year of the study.

**Trichilia septentriionalis** C.DC. (code 180)

Vernacular name: Jataúba vermelha.

Distribution: Central America, Amazon and Guianas.

No regular flowering or fruiting was observed. Figure 5.84.

![Figure 5.80. Phenology of *Carapa guianensis*.](image-url)
Figure 5.81. Phenology of *Guarea kunthiana*.

Figure 5.82. Phenology of *Guarea macrophylla*.
Figure 5.83. Phenology of *Guarea purusana*.

Figure 5.84. Phenology of *Trichilia septentrionalis*.
5.11. MYRISTICACEAE

The Myristicaceae or the nutmeg family consists of 16 genera and 73 species of mainly small to large trees, occurring in the old and new world (Record & Hess 1943, Rodrigues 1980). Most species are dioecious although remnants of the opposite sex are usually present.

The phenology of fruit dispersal was studied by Howe and Kerck (1981) for Virola surinamensis. However, the similarity of the fruits within this family allows for extrapolation on the fruit dispersal of other species.

Table 5.14. Species of Myristicaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irvanthera sagotiana</td>
<td>38</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Virola flexuosa</td>
<td>1</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Virola michelii</td>
<td>50</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>89</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic; A= Acyclic

Irvanthera sagotiana (Bentham) Warb. (code 358)

Vernacular name: Ucuubaran.

Distribution: Northern South America.

Flowering occurred from August-October, in September, April-July and August-January, with a large distinct peak in August of the third year. Fruiting regular but highly extended. Figure 5.85.
Virola flexuosa A.C. Smith (code 354)
Vernacular name: Ucuúba branca.
Distribution: Lower Amazon and Guianas.
Rare species at Jari. Only one individual was observed. It seems to flower from May-September. Fruiting was observed in July of the third year of study.

Virola michelii Heckel (code 356)
Vernacular name: Ucuúba preta, ucuúba vermelha.
Distribution: Amazon and Guianas.
One of the commonest tree species at Jari. Flowering regular, with peak in August. Fruiting also regular but extended. Figure 5.86.
Figure 5.85. Phenology of *Iryanthera sagotiana*.

Figure 5.86. Phenology of *Virola michelii*.
5.12. PALMAE

The Palmae is a natural family of woody monocotyledons, with 212 genera and roughly 2,500 species restricted to the tropics and subtropics. The monopodial stem of the palms with relatively uniform growth patterns offers an interesting opportunity to evaluate morphological constraints on reproductive phenology (DeSteven et al. 1987).

Table 5.15. Species of Palmae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oenocarpus bacaba</td>
<td>17</td>
<td>Zoochory</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Socratea exorrhiza</td>
<td>8</td>
<td></td>
<td>A. Gregarious</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic; A = Acyclic

Oenocarpus bacaba Mart. (code 065)

Vernacular name: Bacaba.

Distribution: Amazon.

Flowering was a bit irregular although a clear peak occurred in August during the first year of the study. Fruiting was extended, starting at the end of the dry season. Figure 5.87.

Socratea exorrhiza (Mart.) H. Wendl. (code 427)

Vernacular name: Paxiúba.

Distribution: Amazon.

Flowering occurred irregularly. Fruiting was extended, starting at the end of the dry season (Figure 5.88).
Figure 5.87. Phenology of *Oenocarpus bacaba*.

Figure 5.88. Phenology of *Socratea exorrhiza*.
5.13. QUIINACEAE

The Quiinaceae is considered an Amazonian family. No recent monograph is available for it although it was studied in the flora of Surinam by Lanjouw and Heerdt (1941). Only two species of trees were found to occur in the area of Jari.

Table 5.16. Species of Quiinaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quiina aff. longifolia</td>
<td>2</td>
<td>Zoochory</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Touroulija guianensis</td>
<td>5</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C = Cyclic; A = Acyclic

Quiina aff. longifolia Spruce ex Pl. & Tr. (code 638)
Vernacular name: Moela de mutum 2.
Distribution: Amazon and Guianas.
Two individuals were observed, neither one flowered or fruited throughout the study.

Touroulija guianensis Aubl. (code 207)
Vernacular name: Moela de mutum.
Distribution: Amazon, mainly in Pará (BR) and French Guiana.
Flowering extended and irregular. Fruiting was observed from March to June but only during the second year of the study. Figure 5.89.
Figure 5.89. Phenology of *Tourouliuia guianensis*.
The Simaroubaceae is a pantropical family of mainly trees or shrubs with bitter bark. No recent monograph is available for it although it was studied in the flora of Surinam by Jansen-Jacobs (1979).

Table 5.17. Species of Simaroubaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number Individuals</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simaba cedron</td>
<td>4</td>
<td>Zoochory</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Simaruba amara</td>
<td>9</td>
<td>C.</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Total</td>
<td>13</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic

Simaba cedron Planchon (code 253)

Synonym: Quassia cedron (Planch.)Baillon

Vernacular name: Para tudo.

Distribution: Amazon and Guianas.

Flowering occurred from December-January during the first year of the study, and from August-November during the third year. Fruiting occurred during the beginning of the wet season. Figure 5.90.

Simaruba amara Aublet (code 224)

Synonym: Quassia amara L.

Vernacular name: Marupá.

Distribution: Amazon and Guianas.

A clear peak of flowering was seen from September to January of the third year of the study. A peak fruiting was also observed in that same year, from December-April. Figure 5.91.
Figure 5.90. Phenology of *Simaba cedron*.

Figure 5.91. Phenology of *Simaruba amara*.
5.15. VOCHYSIACEAE

The family Vochysiaceae consists of about 180 species of mainly trees or shrubs which occurs in tropical South and Central America (Stafleu 1952-1954).

Table 5.18. Species of Vochysiaceae studied

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Ind.</th>
<th>Dispersal Type</th>
<th>Phenology Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erisma laurifolium</td>
<td>1</td>
<td>Pterochory</td>
<td>C. Pluriannual</td>
</tr>
<tr>
<td>Erisma sp. nov.</td>
<td>2</td>
<td>&quot;</td>
<td>A. Greggarious</td>
</tr>
<tr>
<td>Qualea albiflora</td>
<td>10</td>
<td>&quot;</td>
<td>C. Biennial</td>
</tr>
<tr>
<td>Qualea coerulea</td>
<td>6</td>
<td>&quot;</td>
<td>A. Rare</td>
</tr>
<tr>
<td>Qualea paraensis</td>
<td>39</td>
<td>&quot;</td>
<td>C. Biannual</td>
</tr>
<tr>
<td>Vochysia obscura</td>
<td>19</td>
<td>&quot;</td>
<td>C. Annual</td>
</tr>
<tr>
<td>Vochysia vismiifolia</td>
<td>17</td>
<td>&quot;</td>
<td>C. Biannual</td>
</tr>
<tr>
<td>Total</td>
<td>94</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: C= Cyclic; A= Acyclic

**Erisma laurifolium** Warm. (code 553)

Synonym: *Qualea laurifolia* Spruce ex Warm.

Vernacular name: Jaboti vermelho.

Distribution: Amazon and Guianas.

Only one individual was observed. It flowered in January and fruited from February-March of the first year of the study.

**Erisma sp. nov.** (code 722)

Vernacular name: Jaboti da flor branca.

Distribution: Jari river basin.

Flowering irregular. Fruiting was observed during April-July of the second year of the study. Figure 5.92.
Qualea albiflora Warm. (code 212)
Vernacular name: Mandioqueira lisa.
Distribution: Amazon and Guianas.
Flowering occurred at the end of the dry season and beginning of the wet season, omitting however the second year. Fruiting was observed at the beginning of the wet season. Figure 5.93.

Qualea coerulea Aubl. (code 734)
Vernacular name: Mandioqueira.
Distribution: Amazon and Guianas.
Of the six individuals observed none flowered or fruited during the three-year study.

Qualea paraensis Ducke (code 213)
Vernacular name: Mandioqueira escamosa.
Distribution: Amazon and Guianas.
Figure 94.

Vochysia obscura Warm. (code 300)
Vernacular name: Quaruba rosa.
Distribution: Amazon and Guianas.
Flowering occurred at the end of the dry season, sometimes extending into the wet season. Fruiting occurred mostly during the wet season. Figure 5.95.

Vochysia visniifolia Spruce ex Warm. (code 528)
Vernacular name: Quaruba cedro da terra firme.
Distribution: Amazon and Guianas.
Flowering occurred at the end of the dry season and beginning of the wet season. Fruiting occurred mostly during the wet season. Figure 5.96.

![Graph showing phenology of Erisma sp. nov.](image)

Figure 5.92. Phenology of *Erisma* sp. nov.
Figure 5.93. Phenology of *Qualea albiflora*.

Figure 5.94. Phenology of *Qualea parvensis*.
Figure 5.95. Phenology of *Vochysia obscura*.

Figure 5.96. Phenology of *Vochysia vismiifolia*.
CHAPTER 6. COMMUNITY PHENOLOGY AND ECOLOGY

6.1. COMMUNITY STRUCTURE AND PHENOLOGY

Before attempting to draw conclusions on a microregion basis it is important to evaluate the degree of ecological variation among the forest communities studied in the present. As pointed out in Chapter 2 the forest sites investigated differed in relation to soil, topography and forest type. A total of eight ecological variables (Table 6.1) were studied through correlation coefficients. They were: (1) altitude (Alt), (2) soil pH (PH), (3) percentage of sand (SAND), (4) percentage of organic matter (OM), (5) exchangeable phosphorus (P), (6) maximum flowering percentage (MAXFL), (7) maximum fruiting percentage (MAXFR) and (8) index of diversity (DIV). The soil variables used were the mean values for the top soil (see Chapter 10 for results of the soil study). Table 6.1 gives the ecological data of the forest communities which were subjected to cluster analysis in order to classify the forest communities of Jari. The index of diversity was calculated by dividing the number of tree species found in each site by the square root of the number of trees sampled. Note that the column of maximum flowering percentage (MAXFL) have some discrepancies in the sense that these values should not be smaller than their counterparts in the column of maximum fruiting percentage (MAXFR). This is due to unrecorded flowering events. However these discrepancies were very small and the values were recorded unchanged.
Table 6.1. Ecological data of the eight forest communities studied at Jari.

<table>
<thead>
<tr>
<th>SITE</th>
<th>ALT (m)</th>
<th>PH</th>
<th>SAND DIV (%)</th>
<th>OM (%)</th>
<th>P (meq/100g)</th>
<th>MAXFL (%)</th>
<th>MAXFR (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANG (Angelim)</td>
<td>77</td>
<td>4.2</td>
<td>87</td>
<td>4.6</td>
<td>4.3</td>
<td>2.9</td>
<td>23</td>
</tr>
<tr>
<td>QUA (Quaruba)</td>
<td>141</td>
<td>4.3</td>
<td>89</td>
<td>3.5</td>
<td>8.0</td>
<td>6.0</td>
<td>34</td>
</tr>
<tr>
<td>MTD (Mt. Dourado)</td>
<td>76</td>
<td>4.4</td>
<td>82</td>
<td>5.3</td>
<td>5.7</td>
<td>5.3</td>
<td>43</td>
</tr>
<tr>
<td>FEL (Felipe)</td>
<td>150</td>
<td>4.7</td>
<td>36</td>
<td>5.5</td>
<td>22.2</td>
<td>4.7</td>
<td>15</td>
</tr>
<tr>
<td>SML (São Militão)</td>
<td>113</td>
<td>4.0</td>
<td>73</td>
<td>5.7</td>
<td>5.0</td>
<td>4.0</td>
<td>22</td>
</tr>
<tr>
<td>PAC (Pacanari)</td>
<td>107</td>
<td>4.2</td>
<td>38</td>
<td>5.9</td>
<td>16.6</td>
<td>4.2</td>
<td>18</td>
</tr>
<tr>
<td>ITA (Itapeuara)</td>
<td>37</td>
<td>4.0</td>
<td>18</td>
<td>6.0</td>
<td>17.4</td>
<td>4.0</td>
<td>30</td>
</tr>
<tr>
<td>IBA (Ibama=Sema)</td>
<td>449</td>
<td>4.7</td>
<td>71</td>
<td>7.5</td>
<td>14.4</td>
<td>4.7</td>
<td>19</td>
</tr>
</tbody>
</table>

The correlation coefficients were calculated by both the Pearson product-moment and the Spearman rank methods. They were used to test the null hypothesis of zero correlation between variables. Both correlation coefficients range from -1.0 to +1.0. The values close to zero indicate little correlation while the values close to -1 or 1 indicate strong correlation. However, because the phenological data are not normal the latter is more appropriate. The Pearson product-moment correlation coefficient, r, makes the usual assumption of a linear relationship between the variables of the communities being compared (Krebs 1989). Exploration of the data through line plotting indicated that the assumption of linearity was unrealistic. Thus the Spearman method was chosen for the analysis since it does not assume that the variables display a linear relationship. This is possible because the Spearman method calculates the correlation coefficients on the ranks of the data rather than the actual data values.
The Spearman rank correlation coefficient procedure used to examine the correlation between the eight community variables listed above is displayed on Table 6.2. In this table, the first line of each pair gives the correlation coefficients while the line below gives the calculated probabilities for a null hypothesis of no correlation between variables.

Table 6.2. Spearman rank correlation coefficients on community variables from Table 6.1, together with the calculated probability for a null hypothesis of zero correlation.

<table>
<thead>
<tr>
<th></th>
<th>ALT</th>
<th>PH</th>
<th>SAND</th>
<th>OM</th>
<th>P</th>
<th>MAXFL</th>
<th>MAXFR</th>
<th>DIV</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALT</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PH</td>
<td>0.63</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.09</td>
<td></td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAND</td>
<td>0.07</td>
<td>0.07</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.87</td>
<td>0.86</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OM</td>
<td>0.19</td>
<td>0.28</td>
<td>-0.81</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.65</td>
<td>0.50</td>
<td>0.01</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0.40</td>
<td>0.67</td>
<td>0.27</td>
<td>0.24</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.33</td>
<td>0.07</td>
<td>0.53</td>
<td>0.57</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAXFL</td>
<td>-0.57</td>
<td>-0.23</td>
<td>0.55</td>
<td>-0.48</td>
<td>0.24</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.14</td>
<td>0.58</td>
<td>0.16</td>
<td>0.23</td>
<td>0.57</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAXFR</td>
<td>-0.68</td>
<td>-0.41</td>
<td>-0.28</td>
<td>0.29</td>
<td>0.18</td>
<td>0.48</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>0.31</td>
<td>0.51</td>
<td>0.49</td>
<td>0.68</td>
<td>0.23</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>DIV</td>
<td>0.10</td>
<td>-0.07</td>
<td>-0.76</td>
<td>0.48</td>
<td>-0.27</td>
<td>-0.45</td>
<td>0.07</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>0.82</td>
<td>0.86</td>
<td>0.03</td>
<td>0.23</td>
<td>0.53</td>
<td>0.26</td>
<td>0.87</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Very few correlations were found among environmental variables, according to Table 6.2. The variable percentage of organic matter (OM) correlated with percentage of sand in soil (SAND). The variable percentage of sand in soil
(SAND) also correlated with diversity index (DIV). The correlation coefficients by the Pearson method differed from those calculated by the Spearman method only in the fact that the variable percentage of sand in soil (SAND) correlated only with organic matter (OM).

In order to evaluate the degree of ecological variation among the forest communities studied in this thesis cluster analysis was performed on the variables displayed in Table 6.1, using the Proc Cluster procedure of SAS-5.18. Three methods were tested: average linkage, complete linkage and single linkage. All methods are based on the usual agglomerative hierarchical clustering procedure. The single linkage method was the best of the three and allowed the four level classification for the forest sites of Jari displayed in Figure 6.1. This method provided the values for the minimum distance between the clusters.

Three models were investigated to test the dependency of the variables 'diversity index' (DIV), 'maximum flowering' (MAXFL) and 'maximum fruiting' (MAXFR) upon the remaining ones. This was done by calculating the mean square error of the linear regression for models with different number of independent variables. The mean square error is the basis for an estimate of the error in fitting the regression line (Snedecor 1956). Each model has several models to explain the relationship between the dependent variable with the independent ones. The best model of each dependent variable is that which uses the least number of independent
variables with the smallest square error accepted. Results of the three models tested are given on Tables 6.3, 6.4 and 6.5.

Figure 6.1. Ecological classification of the forest sites of Jari through cluster analysis.
Table 6.3. Mean square error for model 1 of 'diversity index' (DIV) as dependent variable.

<table>
<thead>
<tr>
<th>No of Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Sq. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>alt</td>
<td>0.35</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>alt, sand</td>
<td>0.65</td>
<td>0.65</td>
</tr>
<tr>
<td>3</td>
<td>alt, sand, om</td>
<td>0.86</td>
<td>0.33</td>
</tr>
<tr>
<td>4</td>
<td>alt, sand, om, pH</td>
<td>0.97</td>
<td>0.08</td>
</tr>
<tr>
<td>5</td>
<td>alt, sand, om, pH, maxfl</td>
<td>0.98</td>
<td>0.09</td>
</tr>
<tr>
<td>6</td>
<td>alt, sand, om, pH, maxfl, maxfr,</td>
<td>0.99</td>
<td>0.00</td>
</tr>
<tr>
<td>7</td>
<td>alt, sand, om, pH, maxfl, maxfr, P</td>
<td>1.00</td>
<td>.</td>
</tr>
</tbody>
</table>

Table 6.4. Mean square error for model 2 of 'maximum flowering' (MAXFL) as dependent variable.

<table>
<thead>
<tr>
<th>No of Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Sq. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>maxfr</td>
<td>0.33</td>
<td>69.98</td>
</tr>
<tr>
<td>2</td>
<td>maxfr, sand</td>
<td>0.84</td>
<td>20.48</td>
</tr>
<tr>
<td>3</td>
<td>maxfr, sand, om</td>
<td>0.94</td>
<td>10.01</td>
</tr>
<tr>
<td>4</td>
<td>maxfr, sand, om, pH</td>
<td>0.96</td>
<td>9.31</td>
</tr>
<tr>
<td>5</td>
<td>maxfr, sand, om, pH, div</td>
<td>0.97</td>
<td>10.62</td>
</tr>
<tr>
<td>6</td>
<td>maxfr, sand, om, pH, div, alt</td>
<td>0.99</td>
<td>0.23</td>
</tr>
<tr>
<td>7</td>
<td>maxfr, sand, om, pH, div, alt, P</td>
<td>1.00</td>
<td>.</td>
</tr>
</tbody>
</table>

Table 6.5. Mean square error for model 3 of 'maximum fruiting' (MAXFR) as dependent variable.

<table>
<thead>
<tr>
<th>No of Ind. Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Square Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>maxfl</td>
<td>0.33</td>
<td>49.95</td>
</tr>
<tr>
<td>2</td>
<td>maxfl, sand</td>
<td>0.85</td>
<td>13.56</td>
</tr>
<tr>
<td>3</td>
<td>maxfl, sand, om</td>
<td>0.95</td>
<td>5.57</td>
</tr>
<tr>
<td>4</td>
<td>maxfl, sand, om, pH</td>
<td>0.96</td>
<td>5.46</td>
</tr>
<tr>
<td>5</td>
<td>maxfl, sand, om, pH, div</td>
<td>0.97</td>
<td>6.88</td>
</tr>
<tr>
<td>6</td>
<td>maxfl, sand, om, pH, div, alt</td>
<td>0.99</td>
<td>0.19</td>
</tr>
<tr>
<td>7</td>
<td>maxfl, sand, om, pH, div, alt, P</td>
<td>1.00</td>
<td>.</td>
</tr>
</tbody>
</table>

For 'diversity index' (DIV) as dependent variable the best fit model was the one which included percentage of sand (SAND), percentage of organic matter (OM), altitude (ALT)
and pH (PH). For 'maximum flowering' (MAXFL) as dependent variable the best fit model was the one which included percentage of organic matter (OM), pH, diversity index (DIV) and maximum fruiting (MAXFR). For 'maximum fruiting' (MAXFR) as dependent variable the best fit model was the one which included organic matter (OM), pH, diversity index (DIV) and maximum flowering (MAXFL). Here, a simpler model omitting diversity index (DIV) could also be considered since the inclusion of the remaining variables adds very little to the model.

6.2. COMMUNITY FLOWERING AND FRUITING

6.2.1. Introduction

This section investigates the proportion of individuals that flower and fruit in each of the eight forest communities studied. The monthly indices used in Figures 6.2 - 6.18, already displayed in Table 5.1, were repeated in the page preceding these figures along with a key to the symbols utilized.

As already mentioned in Chapter 2 the climate of Jari is not uniform throughout the year due to a mild dry season which takes place between August and December. Figure 6.2 shows the combined flowering and fruiting phenologies of the 1508 trees investigated. Flowering occurred throughout the year but showed a distinct peak towards the end of the
dry season. During the first year of the study (1987-88) the flowering peak occurred in January which is normally the first month of the rainy season, but not so in that particular year, when the dry season had extended until January (Figure 2.3). The overlap flowering of each of the eight forests studied is shown in Figure 6.3. Fruiting also occurred throughout the year but showed a distinct peak during the rainy season (Jan-Jul). The fruiting peaks were more evident during 1987-88 and 1989-90.

Flowering in tropical trees lasts a very short period of time when compared with fruiting. For this reason sometimes flowering events passed undetected in the monthly observations of this study and can be inferred by the larger number of fruiting events as shown in Figure 6.2.

Flowering and fruiting were also calculated according to seasonal pattern of wet, dry, transition wet to dry and transition dry to wet (Table 6.6).

<table>
<thead>
<tr>
<th>SEASON</th>
<th>FLOWERING</th>
<th>FRUITING</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet</td>
<td>16</td>
<td>59</td>
</tr>
<tr>
<td>Wet-Dry</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Dry</td>
<td>38</td>
<td>9</td>
</tr>
<tr>
<td>Dry-Wet</td>
<td>72</td>
<td>53</td>
</tr>
</tbody>
</table>

In the seasonal forests of the Jari river basin most trees flowered either during the dry season or between the end of the dry and beginning of the wet season. Fruiting occurred
more often during the wet season and during the transition between the wet and the dry season. Very few species of trees fruited during the dry season (Table 6.6).

Two questions that are always asked about fruiting are firstly whether it is controlled by its own mechanism and secondly the extent to which it is dependent on flowering. Fruiting is a phenomenon which necessarily follows flowering and is bound to be influenced by it. The fruiting and flowering curves were very similar as shown in Figures 6.2 to 6.12. The dependency of flowering and fruiting upon one another is tested in Chapter 7 by regression analysis.

6.2.2. Flowering and fruiting variation among the eight communities.

The flowering of each of the eight forests studied is illustrated in Figure 6.3. This figure indicates a clear superposition of the flowering curves of all the forests studied. One variable that is widely used in phenology is the peak of flowering or fruiting events, which have been referred by some as ‘mean’ phenology. In this section we examine the peaks of flowering of each forest community studied to see whether or not is a significant difference between them. However, the median is used rather than the mean since the former is a more adequate measure of location for non-normally distributed data (Campbell 1989, Krebs 1989).
The fruiting of each of the eight forests studied is illustrated in Figure 6.4. Like the case of flowering this figure indicates a clear superposition of the fruiting curves of all the forests studied. Figures 6.5 to 6.12 show the flowering and fruiting percentage of each of the eight forests studied. An examination of the peaks or median of fruiting of each forest community studied allowed to separate the peaks displayed in Table 6.7.

### Table 6.7. Month of peak flowering and fruiting in the eight Jari forests studied.

<table>
<thead>
<tr>
<th>Forest Community</th>
<th>Year: 87/88</th>
<th>88/89</th>
<th>89/90</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angelim (Ang)</td>
<td>Nov</td>
<td>Apr</td>
<td>no peak</td>
</tr>
<tr>
<td>Quaruba (Qua)</td>
<td>Jan</td>
<td>Feb</td>
<td>Nov  Mar</td>
</tr>
<tr>
<td>Monte Dourado (MtD)</td>
<td>Jan</td>
<td>Mar</td>
<td>Nov  Mar</td>
</tr>
<tr>
<td>Felipe (Fel)</td>
<td>Jan</td>
<td>Feb</td>
<td>no peak</td>
</tr>
<tr>
<td>São Militão (Sml)</td>
<td>Dec</td>
<td>Feb</td>
<td>no peak</td>
</tr>
<tr>
<td>Pacanari (Pac)</td>
<td>Dec</td>
<td>Mar</td>
<td>Nov  -</td>
</tr>
<tr>
<td>IBAMA (Iba)</td>
<td>Jan</td>
<td>Apr</td>
<td>no peak</td>
</tr>
<tr>
<td>Itapeuara (Ita)</td>
<td>Nov</td>
<td>Jan</td>
<td>Nov  Jan</td>
</tr>
</tbody>
</table>

6.2.3. **Conclusion.**

The major result of the present work as far as community phenology is concerned is that only a small percentage of the individual trees in a forest ever flower or fruit even during the highest period of flowering and fruiting activity. In the eight native forests studied at Jari the average percentage of trees that entered the flowering stage at any one month was 20 per cent. The highest value of 43 percent occurred only at one of the dry open forests.
The low fertility percentage of tropical trees under primary forest conditions was also reported for in French Guiana by Sabatier (1985) and by Mori and Prance (1987a). It must also be emphasized that in Jari there were many trees that flowered but never bore fruits. The combined flowering phenology of the eight native forests studied showed a maximum of 20 and a minimum of one percent of individuals flowering at any one month of the three years of observations. These results are shown in figures 6.5 to 6.12 for the eight forest sites. The six phenology phases studied, including two reproductive and four vegetative ones, are all summarized on Figure 6.18.

The low proportion of flowering in the tree species studied can be interpreted as an adaptation to the stable environment found in a primary forest. Such stable environment would promote an economy in reproductive cost in favour of vegetative growth. An evidence for this is the fact that in Jari most, if not all, trees occurring near roads showed copious flowering and fruiting. Another evidence is the fact that many of the trees restricted their flowering to the sections of canopy that received direct sun light.
6.3. COMMUNITY VEGETATIVE PHENOLOGY.

6.3.1. Introduction

This Section covers the number of individuals displaying the four vegetative classes studied in each of the eight forest sites. The vegetative classes studied were: old canopy, shedding, flushing and entire new canopy. The phenological data obtained for each of the forest sites studied was superimposed for visual comparison of the patterns (Figures 6.14 to 6.17). The vegetative phenology of the microregion of Jari is inferred from the combined data of all 1508 trees observed (Figure 6.13). Flushing (Figure 6.16) was hardly observed since new leaves tend to appear gradually and mixed with existing old leaves. Figure 6.14 shows the situation of old canopy in the eight forests studied. By comparing this figure with the rainfall of Jari during the same period (Figure 2.4) one can see the resemblance between the two. The illustration of the shedding condition (Figure 6.15) was the exact opposite to the old canopy condition shown in Figure 6.14 and coincided with the months that had the least rainfall. The relationship between rainfall and the state of the canopy is investigated in Chapter 7 through regression analysis.

The measure of how many trees showed entire new canopy (Figure 6.17) is also interesting since it reflects the environmental parameters of the microregion as a whole which in turn can be compared with other microregions
within the Amazon itself. Figure 6.18 shows the summation of the six phenological phases investigated, being four vegetative and two reproductive.

6.3.2. Conclusion

It is well recorded in the literature that although the tropical rain forest is evergreen its trees show various patterns of leaf fall (Janzen 1975). The seasonal climate found in the microregion of Jari influences the shedding time of most tree species observed by making it more pronounced during the dry season.

According to the way of leaf shedding the trees can be classified into three types. The most common type found in Jari includes those trees which shed only part of their canopies at one time, never becoming completely leafless. These trees are called semi-evergreen or semi-deciduous. Most trees found in Jari fall under this category. Secondly, there are a small number of tree species which lose their entire canopy during the dry season. These are called deciduous trees even though their leafless condition lasts only a very short period. Examples of trees that exhibited deciduous behaviour at Jari are Anacardium spruceanum, Tapirira spp., Eriotheca globosa, Parkia spp., Connarus perrottetii, Couratari guianensis and some species of Inga. The third type are trees are those whose leaves are substituted gradually throughout the year, without a noticeable increase in shedding during the dry season.
These are referred to as evergreen trees. Examples are *Tetraena panamensis*, *Protium* spp., *Vantanea parviflora* and *Pentaclethra macroloba*.

Finally, there are entire plant families which are more adapted to seasonal climate such as the Vochysiaceae. Species of this family occur mainly in the two dry forests studied, Angelim and Quaruba. One of its species, *Vochysia vismiifolia* sheds not only leaves but entire branches as well.

---

### Key to the monthly indices utilized

<table>
<thead>
<tr>
<th>INDEX</th>
<th>MONTH</th>
<th>YEAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-8</td>
<td>May-December</td>
<td>1987</td>
</tr>
<tr>
<td>9-20</td>
<td>January-December</td>
<td>1988</td>
</tr>
<tr>
<td>21-32</td>
<td>January-December</td>
<td>1989</td>
</tr>
<tr>
<td>33-36</td>
<td>January-April</td>
<td>1990</td>
</tr>
</tbody>
</table>

---

### Key to the figure symbols utilized

<table>
<thead>
<tr>
<th>SYMBOL</th>
<th>PHENOLOGY PHASE</th>
</tr>
</thead>
<tbody>
<tr>
<td>✿</td>
<td>Flowering</td>
</tr>
<tr>
<td>♂</td>
<td>Fruiting</td>
</tr>
<tr>
<td>🌃</td>
<td>Old Canopy</td>
</tr>
<tr>
<td>▲</td>
<td>Leaf Shedding</td>
</tr>
<tr>
<td>++</td>
<td>Flushing</td>
</tr>
<tr>
<td>✶</td>
<td>Entire New Canopy</td>
</tr>
</tbody>
</table>
Figure 6.2. Combined reproductive phenology of trees in the Jari region.
Figure 6.3. Flowering phenology of trees in eight forest sites at Jari.
Figure 6.4. Fruiting phenology of trees in eight forest sites at Jari.
Figure 6.5. Flowering and fruiting phenology of the Angelim forest.
Figure 6.6. Flowering and fruiting phenology of the Quaruba forest.
Figure 6.7. Flowering and fruiting phenology of the Monte Dourado forest.
Figure 6.8. Flowering and fruiting phenology of the Felipe forest.
Figure 6.9. Flowering and fruiting phenology of the São Militão forest.
Figure 6.10. Flowering and fruiting phenology of the Pacanari forest.
Figure 6.11. Flowering and fruiting phenology of the Ibama forest.
Figure 6.12. Flowering and fruiting phenology of the Itapeuara forest.
Figure 6.13. Vegetative phenology of Jari trees.
Figure 6.14. Old canopy phenology of Jari trees.
Figure 6.15. Leaf shedding phenology of Jari trees.
Figure 6.16. Leaf flushing phenology of Jari trees.
Figure 6.17. Entire new canopy phenology of Jari trees.
Figure 6.18. Combined summary of the six phenology phases studied at Jari.
CHAPTER 7. FACTORS THAT INFLUENCE TREE PHENOLOGY

7.1. GENETICS

7.1.1. Introduction

From an ecological point of view, each individual is genetically unique or at least unique with respect to its location. Therefore the ecological role of a species can only be determined by the properties of its individuals (Hallam et al. 1990). In order to investigate the genetical influence on phenology this chapter looks at the flowering and fruiting phenology of the individuals of ten species of trees which had a large sample of individuals. The species listed in Table 7.1 were chosen for this study due to the fact that each occur in only one forest. The only exception, Guarea kunthiana, occurs in two very close and similar forests, but only the larger population was included in the synchrony calculation.

7.1.2. Variation Among Individuals

The study of the phenological variation among individuals and populations is done through measures of the flowering and fruiting synchrony. To investigate synchrony among individuals of a population, we chose a method devised by Primack (1980) and modified by Augspurger (1983). This method, which was originally devised for shrubs, simply measures overlap on all days an individual shrub shows at
least one open flower. To adapt this method to tropical
trees we opted to use months instead of days and to
disregard the maturity stage of the flowers. For the
synchrony calculation only those individuals that actually
entered a flowering and fruiting stage were analysed.

Method for calculating synchrony (adapted from Primack 1980
and Augspurger 1985).

i) Synchrony of a given individual with its conspecifics:

$X_i$, the index of synchrony for individual $i$, is defined as:

$$X_i = \left(\frac{1}{n-1}\right) \left(\frac{1}{f_i}\right) \sum_{j=1}^{n} e_{j|i}$$

where,

$e_{j|i} = \text{number of months both individual } i \text{ and } j \text{ are}
\text{flowering synchronously, } j \neq i;$

$f_i = \text{number of months individual } i \text{ is flowering};$

$n = \text{number of individuals in population that enter in}
\text{flowering during the studied period;}

When $X = 1.0$, perfect synchrony occurs, i.e., all
flowering months of individual $i$ overlap with flowering
months of each individual, $j \neq i$ in the population.

When $X = 0.0$, no synchrony occurs, i.e., no overlap
occurs among any of the flowering days of individual $i$ and
each individual, $j \neq i$ in the population.
ii. Synchrony of the population:

\[
Z, \text{ the index of population synchrony, is defined as:} \\
Z = \left( \frac{1}{n} \right) \sum_{i=1}^{n} x_i \\
\]

where \( x_i \) is synchrony of individual \( i \) with its conspecifics from part \( i \) (above).

---

**Table 7.1. Index of flowering synchrony of individuals and populations of ten tropical tree species.**

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>Specie</th>
<th>INDEX OF SYNCHRONY</th>
<th>INDEX OF SYNCHRONY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>INDIVIDUAL</td>
<td>POPULATION</td>
</tr>
<tr>
<td>ANACARDIACEAE</td>
<td>Tapirira sp. nov.</td>
<td>0.0,0.25,0,0</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>T. peckoltiana</td>
<td>0.66,0.66,0.16,0.5</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Thrysodium guianense</td>
<td>0.65,0.79,0.65,0.56,0.62,0.73,0,45,0.37,0.57,0.35</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>T. spruceanum</td>
<td>0.5,0,0.5,0.5,0.5</td>
<td>0.40</td>
</tr>
<tr>
<td>LECYTHIDACEAE</td>
<td>Lecythis corrugata (none fruited)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L. lurida</td>
<td>0.71,0.14,0,0.14,0.07,0.36,0.38,0.71</td>
<td>0.31</td>
</tr>
<tr>
<td>MELIACEAE</td>
<td>Guarea kunthiana</td>
<td>0.06,0.10,0,0.40,0.12,0.40</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>G. macrophylla (none flowered)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VOCHYSIACEAE</td>
<td>Qualea coerulea (none flowered)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Q. albiflora</td>
<td>0.41,0.50,0.33,0.33,0.16,0.0,0.33</td>
<td>0.30</td>
</tr>
</tbody>
</table>
Table 7.2. Index of fruiting synchrony of individuals and populations of ten tropical tree species.

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>INDEX OF SYNCHRONY</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SPECIES</td>
<td>INDIVIDUAL</td>
</tr>
<tr>
<td>ANACARDIACEAE</td>
<td>Tapirira sp. nov.</td>
<td>0.0,0.08,0,0,1</td>
</tr>
<tr>
<td></td>
<td>T. peckoltiana</td>
<td>0.8,0,0,0,0.57</td>
</tr>
<tr>
<td></td>
<td>Thyrsodium guianense</td>
<td>0.4,0.42,0.5,0.5,0.42,0,0.35,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.3,0.4,0,0.25,0.20,0.45</td>
</tr>
<tr>
<td></td>
<td>T. spruceanum</td>
<td>0,1,0.5,1,0</td>
</tr>
<tr>
<td>LECYTHIDACEAE</td>
<td>Lecythis corrugata</td>
<td>0,0,0,0</td>
</tr>
<tr>
<td></td>
<td>L. lurida</td>
<td>0.69,0.69,0.69,0.08,0.69,0.75,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.69,0.75,0</td>
</tr>
<tr>
<td>MELIACEAE</td>
<td>Guarea kunthiana</td>
<td>0.13,0.33,0.06,0.16</td>
</tr>
<tr>
<td></td>
<td>G. macrophylla</td>
<td>0.75,1.0,0,0.21</td>
</tr>
<tr>
<td>VOCHYSIACEAE</td>
<td>Qualea coerulea</td>
<td>(none fruited)</td>
</tr>
<tr>
<td></td>
<td>Q. albiflora</td>
<td>0,0,0</td>
</tr>
</tbody>
</table>

Before proceeding with the interpretation of the synchrony results, it must be noted that many individual trees did not flower each year and that there were several which remained on the vegetative stage throughout the 36 months of this study.

According to the results shown in Tables 7.1 and 7.2, flowering synchrony was much less pronounced than fruiting synchrony. This can be attributed to a larger number of variables affecting flowering as well as to the reproductive biology of each species. For instance, it is thought that hermaphroditic species tend to be more asynchronous than dioecious species since asynchrony is thought to reduce geitonogamy and promote outcrossing by forcing pollinators to move between plants (Rathcke & Lacey 234).
1985). By the same token, monoecious plants are thought to be less synchronous than dioecious since within an individual plant the female phase may be separated from the male phase by a month or longer, to promote outcrossing (Rathcke & Lacey 1985).

Accordingly, there seem to be advantages in variation of flowering phenology within individuals of the same species. The fact that perfect synchrony was never found is evidence for the genetic variability that exists between individuals of a population. Such differences between individuals that do, and the larger number of individuals that do not, enter flowering constitutes strong evidence that the genetical make up of a plant plays a very important role in its flowering and fruiting phenology.

7.2. ENVIRONMENT

7.2.1. Variation Among Populations

There has been much debate concerning the exogenous versus endogenous control of flowering and fruiting in tropical trees. Many authors have speculated on which are the cues that trigger flowering in tropical trees. Those which attribute flowering to environmental causes have suggested rainfall (Augspurger 1983) or photoperiod (Alvim & Alvim 1978), while others attribute flowering to internal

Environmental aspects such as pluviometry and photoperiod have been pointed as proximate causes of flowering phenology. In this study it is assumed that the climate of all the forests studied is constant since they are all located within one microregion where the distance between the two most distant forests is less than one degree of latitude. No significant difference of rainfall occurs between the various climatic stations of Jari (Correa et al. 1989). Thus soil (and its components) is the only significant environmental factor that could be used to separate the forests studied.

In order to study the environmental influence on phenology we investigated the fruiting phenology of 10 tree species in different forest communities (Table 7.3). There are two reasons for choosing to compare fruiting rather than flowering. Firstly, flowering duration can be so short that it may go unnoticed in monthly observations. Secondly, the fruiting curves and peaks of individual trees resembles closely those of flowering as shown in Figures 6.4 to 6.11.

The role of the environment can also be deduced by comparing the phenology of various communities (Chapter 6, Figures 6.2 and 6.3). In this chapter we will test the null hypothesis that the fruiting phenologies of different populations of the same species of trees are the same. The
measure of central distribution adopted here was the median which permits location tests through analysis of variance of ranks. This statistical method was chosen instead of the more common anovar due to the skewedness of the flowering and fruiting phenologies as seen in all the graphics of Chapter 5. Specifically, the Wilcoxon's test will be used for comparing the medians of two statistical populations (species), while for comparing three or more statistical populations the method chosen is the Kruskal-Wallis.

Table 7.3. Comparison of the fruiting phenology between populations of ten tree species.

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>SPECIES</th>
<th>CHISQ</th>
<th>DF</th>
<th>P&gt;CHISQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>BURSER.</td>
<td><em>Protium sagotianum</em></td>
<td>13.43</td>
<td>4</td>
<td>0.0093</td>
</tr>
<tr>
<td>CHRYSOB.</td>
<td><em>Hirtella bicornis</em></td>
<td>5.95</td>
<td>5</td>
<td>0.3114</td>
</tr>
<tr>
<td>LECYTH.</td>
<td><em>Eschweilera coriacea</em></td>
<td>1.60</td>
<td>2</td>
<td>0.4500</td>
</tr>
<tr>
<td>MELIAC.</td>
<td><em>Carapa guianensis</em></td>
<td>3.36</td>
<td>3</td>
<td>0.2861</td>
</tr>
<tr>
<td>LEGUM.</td>
<td><em>Dinizia excelsa</em></td>
<td>26.96</td>
<td>3</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td><em>Marmaroxylon racemosum</em></td>
<td>20.40</td>
<td>6</td>
<td>0.0011</td>
</tr>
<tr>
<td></td>
<td><em>Pseudopiptadenia psilostachya</em></td>
<td>2.97</td>
<td>4</td>
<td>0.5632</td>
</tr>
<tr>
<td>MYRIST.</td>
<td><em>Iryanthera sagotiana</em></td>
<td>12.45</td>
<td>4</td>
<td>0.0143</td>
</tr>
<tr>
<td></td>
<td><em>Virola michellii</em></td>
<td>58.40</td>
<td>5</td>
<td>0.0001</td>
</tr>
<tr>
<td>VOCHYS.</td>
<td><em>Qualea paraensis</em></td>
<td>10.92</td>
<td>3</td>
<td>0.0122</td>
</tr>
</tbody>
</table>

CHISQ = test statistic; DF = degrees of freedom= nQ of populations - 1; P= probability of observed test statistic.

As pointed out before soil (and its factors) is the only environmental variable separating the eight forests studied. Table 7.3 shows that in only 4 out of 10 species of trees the null hypothesis stating that the fruiting phenologies of different populations of the same species of trees were the same was not rejected. This implies indirectly that populations of such trees did not vary in fruiting phenology between sites. They were: *Hirtella*
bicornis, Eschweilera coriacea, Carapa guianensis, and Piptadenia communis, which are widespread well adapted species. The fact that 6 out of 10 species had different fruiting phenologies in different sites suggests that soil could be an important factor in determining the phenological pattern of a tree species. The drier forests, Angelim, Quaruba and Monte Dourado, have unconsolidated sandy soils which hold less water than the more consolidated clay soils of the remaining forests and therefore would face an earlier water depletion during the dry season than the latter. Therefore the same tree species would flower earlier when occurring in the dry forests (Angelim, Quaruba and Monte Dourado) than when occurring in any of the remaining forests. Indeed the species which showed significant differences in fruiting phenologies between sites were those whose occurrence included these dry forests.

Finally it must be pointed out that although the variation found between populations is indicative of environmental influence it may also be part of the genetic load of the species. Therefore, both genetics and the environment have an effect on phenology. The environment could be considered the proximate cause while the genetic load of the species would be the ultimate cause, recognized and historically controlled by the environment.
7.2.2. **The Influence of Rainfall and Temperature on Phenology**

This section investigates the relationship among the variables rainfall (R), temperature (T), flowering (FL), fruiting (FR), old canopy (OC) and entire new canopy (E). Firstly, correlation coefficients were calculated and the results used to verify the correlations between such variables (Tables 7.4 and 7.5). Here the correlation coefficients were calculated by both the Pearson product-moment and Spearman rank methods. The data were analysed by means of linear regression techniques in order to detect the dependency of each phenological variable (flowering/FL, fruiting/FR, old canopy/OC and entire new canopy/E) on the two environmental variables (rainfall/R and temperature/T) as well as on the other phenological variables.

Table 7.4 gives the Spearman correlation coefficients of each variable. The variable 'old canopy' correlated with 'entire new canopy', flowering, rainfall and temperature. The variable 'entire new canopy' correlated with 'old canopy', 'flowering' and 'rainfall'. The variable 'flowering' correlated with 'entire new canopy' 'rainfall' and 'temperature'. The variable 'fruiting' correlated only with 'rainfall'. The variable 'rainfall' correlated with 'old canopy', 'entire new canopy', 'flowering' and 'temperature'. The variable 'temperature' correlated with 'old canopy', 'flowering' and 'rainfall'. Table 7.5 provides the correlation coefficients of the same variables.
using the Pearson method. Less correlation was found through the Pearson method than through the Spearman rank correlation method.

Table 7.4. Spearman rank correlation coefficients on environmental and phenological variables, together with the calculated probability for a null hypothesis of zero correlation.

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>E</th>
<th>FL</th>
<th>FR</th>
<th>R</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>1.00</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>-0.88</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>-0.59</td>
<td>0.51</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>FR</td>
<td>-0.04</td>
<td>0.15</td>
<td>0.23</td>
<td>1.00</td>
<td>0.81</td>
<td>0.37</td>
</tr>
<tr>
<td>R</td>
<td>0.55</td>
<td>-0.48</td>
<td>-0.69</td>
<td>0.30</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>T</td>
<td>-0.47</td>
<td>0.30</td>
<td>0.55</td>
<td>-0.18</td>
<td>-0.60</td>
<td>1.00</td>
</tr>
</tbody>
</table>

240
Multiple regression analysis on the correlation coefficients obtained by the Spearman method was carried out in order to select which variables best explained the phenology of tropical trees. The four phenological phases — flowering, fruiting, old canopy and entire new canopy — were treated as dependent variables, and each one was compared not only with the independent variables rainfall and temperature but also with the remaining phases. A summary of the results is given in Table 7.6.

Table 7.6. Mean square error for model of 'flowering' (FL) as dependent variable.

<table>
<thead>
<tr>
<th>NQ of Ind. Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Square Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>rainfall</td>
<td>0.33</td>
<td>19.86</td>
</tr>
<tr>
<td>2</td>
<td>rainfall, fr</td>
<td>0.51</td>
<td>15.12</td>
</tr>
<tr>
<td>3</td>
<td>rainfall, fr, e</td>
<td>0.52</td>
<td>15.33</td>
</tr>
<tr>
<td>4</td>
<td>rainfall, fr, e, oc</td>
<td>0.57</td>
<td>13.97</td>
</tr>
<tr>
<td>5</td>
<td>rainfall, fr, e, oc, temp</td>
<td>0.57</td>
<td>14.37</td>
</tr>
</tbody>
</table>
Table 7.7. Mean square error for model of 'fruiting' (FR) as dependent variable.

<table>
<thead>
<tr>
<th>NQ of Ind. Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Square Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>fl</td>
<td>0.07</td>
<td>33.77</td>
</tr>
<tr>
<td>2</td>
<td>fl, rainfall</td>
<td>0.30</td>
<td>26.17</td>
</tr>
<tr>
<td>3</td>
<td>fl, rainfall, e</td>
<td>0.38</td>
<td>23.96</td>
</tr>
<tr>
<td>4</td>
<td>fl, rainfall, e, oc</td>
<td>0.40</td>
<td>24.06</td>
</tr>
<tr>
<td>5</td>
<td>fl, rainfall, e, oc, temp</td>
<td>0.40</td>
<td>24.77</td>
</tr>
</tbody>
</table>

Table 7.8. Mean square error for model of 'old canopy' (OC) as dependent variable.

<table>
<thead>
<tr>
<th>NQ of Ind. Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Square Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>rainfall</td>
<td>0.28</td>
<td>506.92</td>
</tr>
<tr>
<td>2</td>
<td>rainfall, fr</td>
<td>0.34</td>
<td>479.34</td>
</tr>
<tr>
<td>3</td>
<td>rainfall, fr, fl</td>
<td>0.34</td>
<td>492.53</td>
</tr>
<tr>
<td>4</td>
<td>rainfall, fr, fl, temp</td>
<td>0.34</td>
<td>507.80</td>
</tr>
</tbody>
</table>

Table 7.9. Mean square error for model of 'entire new canopy' (E) as dependent variable.

<table>
<thead>
<tr>
<th>NQ of Ind. Variables</th>
<th>Ind. Variables</th>
<th>R-square</th>
<th>Mean Square Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>rainfall</td>
<td>0.22</td>
<td>42.73</td>
</tr>
<tr>
<td>2</td>
<td>rainfall, fr</td>
<td>0.30</td>
<td>39.64</td>
</tr>
<tr>
<td>3</td>
<td>rainfall, fr, temp</td>
<td>0.31</td>
<td>39.96</td>
</tr>
<tr>
<td>4</td>
<td>rainfall, fr, temp, fl</td>
<td>0.32</td>
<td>40.64</td>
</tr>
</tbody>
</table>

Regression analysis showed that all four phenological phases tested - old canopy, entire new canopy, flowering and fruiting - correlated with rainfall, but not with temperature. Some correlation was also found amongst the phenological phases themselves as shown on Tables 7.6, 7.7, 7.8 and 7.9.
CHAPTER 8. PHENOLOGICAL MODELLING

8.1. THEORETICAL BACKGROUND

The results obtained from the flowering and fruiting phenologies of the trees observed in the present study can be used to build formal mathematical models.

A mathematical model is any system of definitions, assumptions, and equations set up to discuss particular physical phenomena (Daintith & Nelson 1989). Biological modelling is defined as the attempt to quantify relations between biological processes (Lieth 1974). This involves predicting and simulating the correlations between, or the causes of, the biological processes and their driving or controlling forces (Lieth 1974). Phenology models must be analyzed over time as well as in space. To interpret the temporal organization one must understand both the timing mechanism of individual organisms and the role of organism interactions in the rate and pattern of development in the wider system (Lieth 1974).

Phenological models in plants are devised according to the type of data available or attainable. Phenological observation of a herb or shrub differs significantly from that of trees. Similarly, observations of trees under primary forest conditions also differ from those of trees under cultivation or even from trees in open disturbed habitats. A herb can be grown in a green house under
controlled conditions where not only a defined environmental variable can be observed at a time but also allowing measurements to be repeated. Phenological data of trees in natural forest conditions can only be derived from observation and does not allow for such experimental design. Phenological patterns of tropical trees also differ from patterns found in temperate forests. Even considering only tall tropical trees major differences can occur according to their habitat. Also, trees growing in disturbed conditions have different phenological patterns than those occurring under primary forest (Sabatier 1985).

Some of the difficulties in studying phenology of tropical trees in undisturbed forests have been mentioned in Section 5 of Chapter 1. Besides the problems of sample size the very high canopies of the tropical rain forest and the inconspicuousness of many flowers and fruits does not permit the easy separation between the various stages of flowering and fruiting. This can be complicated further when a large number of species are being studied. As a result the data collected for each individual tree observed is a time series of 36 monthly observations. The data for particular species result from subsequent countings of each of the phenological phases of its individuals.

Tropical rain forest tree phenology involves the modelling of count data, typically with a large number of zero observations for which the modelling assumption of statistical normality is inappropriate. Many studies of
tropical phenology have been based on the species level without accounting for the non-displaying of the phenology phenomena by some or even most individuals of a population. This is wrong for it ignores the genetic polymorphism of a species ability to enter a particular phase. The following empirical model, although still a rudimentary one, accounts for the non-occurrence as well as the occurrence of a particular phenological phase of tropical trees.

8.2. GENERAL MODEL OF TROPICAL TREE PHENOLOGY

The present chapter presents some graphical models to describe the major patterns of flowering phenology of tropical tree species. Before proceeding it is important to make a distinction between species pattern and individual tree pattern. In this thesis the term species is used according to the biological species concept. Therefore, the graphic models presented refer to populations.

The literature contains many attempts to classify patterns of flowering phenology in tropical plants. One of the first was proposed by Gentry (1974) and is shown in Chapter 4, Section 4.2. Other patterns or models of flowering phenology in tropical plants are found in Alvim (1964), Sabatier & Puig (1986), Mori & Prance (1987a), etc. It must be pointed out that the patterns suggested by Gentry (1974) were devised to describe the phenology of the Bignoniaceae, which is mainly a family of lianas rather
than trees. In order to use Gentry's flowering patterns for trees one must make clear that they refer to patterns of individual trees rather than to particular species.

The basic model to describe the phenological pattern of tropical tree species has three major components:

(1) Observed periodicity of flowering;
   Periodicity is the frequency of individuals flowering within a period of time. In our case we chose the 36 months of observations.

(2) Percentage of flowering occurrence;
   The second component, percent of event occurrence, permits the detection of the height and shape of a flowering curve if one occurs.

(3) Seasonal factor;
   Seasonal factor is any environmental variable that occurs seasonally at equally spaced time intervals. As mentioned earlier in Chapter 1, Section 1, even small climatic changes that take place in the tropics and sub-tropics may influence the various phenological cycles of plants.

As described in Chapter 2 the studied area in the Jari river basin shows two distinct seasons, a wet one between January and July and a dry one between August and December (Figure 2.2).
The above components are interdependent and each one depends on the occurrence of the preceding one. The simplest variation of the model is that in which an individual tree or a group of individuals of the same species do not enter the phenological phase.

The following two components, periodicity and seasonality permit to fit two harmonic curves in species represented by a large number of individuals. Although seasonality has been described in almost all studies in tropical phenology no attempt has been made to model it and to compare population or species groups to see whether or not they have the same seasonal pattern.

The ecological role of a species can only be determined by the properties of its individuals (Hallam et al. 1990). In this sense, if a forecast of the ability of a population to enter flowering or fruiting is to be successful it must account for the distribution of individual capabilities of changing from a vegetative state to flowering or from flowering to fruiting.

8.3. SPECIFIC MODELS OF TROPICAL TREE PHENOLOGY

Our study on the flowering and fruiting phenology of individual species of trees showed some patterns that could probably fit most species of tropical seasonal forests.
Figures 8.1 to 8.6 illustrate the patterns described in Table 8.1.

Table 8.1. Models of flowering phenology of tree species found in seasonal neotropical forests.

1. CYCLIC or SEASONAL
   1.1. Annual - Occurs regularly once each year.
   1.2. Biennial - Occurs regularly every two years.
   1.3. Pluriannual - Occurs at 3 or more years interval.

2. ACYCLIC or NONSEASONAL
   2.1. Gregarious - Occurs when the individual trees flower at random and without synchrony.
   2.2. Massive-extended - Occurs when an environmental cause (e.g. after a heavy rain during the dry season) triggers the synchronous flowering of several individuals while others prolong the process by flowering more or less sequentially.
   2.3. Rare or Unusual - Occurs when only a very small number of individuals ever enter the flowering stage over a three year or longer period. Includes monocarpy.

The visual inspection of the plotted data for the species studied allowed the classification of their phenological models (Tables 5.2 to 5.16).

8.4. CONCLUSION

Although the models suggested in Table 8.1. refer to flowering, the same models can be adjusted for fruiting. It has been shown that fruiting curves and peaks of individual trees resemble closely those of flowering (Figures 6.4-6.11).

The formal fitting, assessment and checking of statistical models to count data such as the ones found in this study
may be investigated by means of log-linear models. This constitutes a novel area and its development will demand an amount of time and effort equivalent to a Ph.D. thesis in the subject of applied statistics (O'Brien 1991 personal communication).

The proposed models of flowering and fruiting phenology for tree species are important for monitoring trees as genetic resources. They allow the prediction of the best time of the year for seed collecting.

Flowering models can be used to characterize the reproductive pattern of a tree species or individual. A longer duration of flowering could indicate obligate outcrossing. However, trees with very large crowns may also show extended flowering and fruiting due to asynchrony between branches (Medway 1972, Hallé et al. 1978, Bawa 1983). A long flowering period is also found in some dioecious plants in which female flowers may show a different phase from the male flowers (Rathcke & Lacey 1985).
Models of Tropical Tree Phenology

1.1. Cyclic or Seasonal - Annual

Figure 8.1. Model of annual flowering phenology.

1.2. Cyclic or Seasonal - Biennial

Figure 8.2. Model of biannual flowering phenology.
Models of Tropical Tree Phenology

1.3. Cyclic or Seasonal - Pluriannual

![Graph showing pluriannual flowering phenology.]

Figure 8.3. Model of pluriannual flowering phenology.

Models of Tropical Tree Phenology

2.1. Acyclic or Nonseasonal - Gregarious

![Graph showing gregarious flowering phenology.]

Figure 8.4. Model of gregarious flowering phenology.
Models of Tropical Tree Phenology

2.2. Acyclic or Nonseasonal - Massive-extended

Figure 8.5. Model of massive-extended flowering phenology.

Models of Tropical Tree Phenology

2.3. Acyclic or Nonseasonal - Rare

Figure 8.6. Model of rare flowering phenology.
CHAPTER 9. COMPARATIVE PHENOLOGY OF CONGENERS

9.1. THE CONGENER PROBLEM IN ECOLOGY

9.1.1. Theoretical Background.

Many of the early naturalists found it intuitive that taxonomically close sympatric species should compete for shared resources and that such competition would be represented not only by aggressive behavioural interactions but also in more subtle interactions such as pollination (Darwin 1859, Robertson 1895, Elton 1927, Waser 1983).

Progress in the study of tropical ecology uncovered the fact that the tropical rain forest could hold a large number of closely allied species under the same environmental conditions (Richards 1969). This fact caused such impact in the scientific community that in March 1944 the British Ecological Society promoted a symposium on the ecology of closely allied species (Hardin 1960).

In order to conform with the Neo-Darwinian paradigm, the coexistence of these closely allied species in the tropical rain forest has been attributed to the development of reproductive isolation between them. Such isolation would be translated into resource or niche partitioning (Fedorov 1966).

The term character displacement was introduced by Brown & Wilson (1956) to describe the result of coevolution between
competing species. The principle of character displacement states that species would evolve under natural selection to increase the differences in the distribution of the character. Therefore, geographic patterns of congeneric and similar species can be used to test the character displacement hypothesis. According to Futuyma & Slatkin (1983) the best evidence for character displacement comes from comparative studies of the behaviour and morphology of species in sympatric and allopatric populations.

The likelihood of closely related plant species sharing pollinators or dispersers has given rise to a hypothesis that the flowering (Stiles 1977, 1978) or fruiting (Snow 1966, 1971) periods of these species were segregated while overlap in resource use would be reduced. In other words, for testing the above model a null hypothesis was devised stating that the pattern of overlap within a community would be no different from that expected by a random arrangement of the species (Snow 1966, 1971, Stiles 1977, 1978, Pleasants 1983, 1990). According to this assumption both flowering and fruiting would be, therefore, cases of character displacement as defined in 4.2. Although the above model has many problems in the definition of the boundaries of the resource axis it is still considered the best available to date (Pleasants 1990).

As pointed out before, phenology must be studied within the hierarchy from individuals, populations, species and congeners. Variation among individuals and populations
individuals was dealt with in Chapter 7 while variation between species was treated in Chapter 5. The present Chapter 9 examines the fruiting phenology of congeneric species subdivided into sympatric and allopatric groups. A higher competition for resources is expected to occur among sympatric rather than among allopatric species.

In the present chapter the null hypothesis that the fruiting phenologies of sympatric and allopatric congeners are the same is tested. For comparison of the medians of two statistical populations (species) we will use the Wilcoxon’s test while for comparing three or more statistical populations the method chosen is the Kruskal-Wallis.

The comparative phenology of congeners in a tropical forest situation is difficult to assess since it requires a large sample of each population studied. For this study the following group of congeneric species were chosen due to the larger number of individuals sampled in each population.

9.2. SYMPATRIC SPECIES

In the present Section we use the Wilcoxon and the Kruskal-Wallis tests to assesses the null hypothesis that there is no difference between the fruiting phenologies of sympatric congeners. The results are listed in Tables 9.1. to 9.5.
Table 9.1. Wilcoxon test for comparing the fruiting phenology between pairs of sympatric species.

<table>
<thead>
<tr>
<th>SPECIES PAIRS (Site)</th>
<th>Z</th>
<th>P &gt; Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guarea macrophylla (Sml)&amp; Guarea kunthiana (Sml)</td>
<td>1.4671</td>
<td>1.1423</td>
</tr>
<tr>
<td>Protium giganteum (Qua)&amp; Protium sagotianum (Qua)</td>
<td>1.0061</td>
<td>0.3144</td>
</tr>
<tr>
<td>Tetragastris panamensis (Ang) &amp; Tetragastris hostmanii (Ang)</td>
<td>1.1319</td>
<td>0.2577</td>
</tr>
<tr>
<td>Vochysia obscura (Qua)&amp; Vochysia vismiifolia (Qua)</td>
<td>-1.4450</td>
<td>0.1485</td>
</tr>
<tr>
<td>Vochysia obscura (Ang) &amp; Vochysia vismiifolia (Ang)</td>
<td>0.1169</td>
<td>0.9069</td>
</tr>
</tbody>
</table>

Z = test statistic; P = probability of observed test statistic.

The result of the test statistic given in Table 9.1 show that there is not enough evidence to reject the null hypothesis of equal fruiting phenology between two sympatric species.

Table 9.2. Kruskal-Wallis test for comparing the fruiting phenology between three sympatric species.

<table>
<thead>
<tr>
<th>SPECIES (Site)</th>
<th>CHISQ</th>
<th>DF</th>
<th>P&gt;CHISQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caryocar glabrum (Ita), Caryocar microcarpum (Ita) &amp; Caryocar pallidum (Ita)</td>
<td>6.28</td>
<td>2</td>
<td>0.0433</td>
</tr>
<tr>
<td>Hirtella bicornis (Fel), Hirtella obidensis (Fel) &amp; Hirtella piresii (Fel)</td>
<td>6.13</td>
<td>2</td>
<td>0.0466</td>
</tr>
<tr>
<td>Protium robustum (Ita), Protium sagotianum (Ita) &amp; Protium opacum (Ita)</td>
<td>3.45</td>
<td>2</td>
<td>0.1786</td>
</tr>
</tbody>
</table>

CHISQ = test statistic; DF = degrees of freedom= nQ of populations - 1; P= probability of observed test statistic.
Table 9.2. shows two significant results, for the first two groups of sympatric species. This means that Caryocar spp. and Hirtella spp. probably have different fruiting phenologies and that the Protium spp. could have similar fruiting phenologies.

Table 9.3. Kruskal-Wallis test for comparing the fruiting phenology between five sympatric species.

<table>
<thead>
<tr>
<th>SPECIES PAIRS (Site)</th>
<th>CHISQ</th>
<th>DF</th>
<th>P&gt;CHISQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protium giganteum (Fel), Protium nitidifolium (Fel), Protium subserratum (Fel), Protium opacum (Fel) &amp; Protium paniculatum (Fel)</td>
<td>13.89</td>
<td>4</td>
<td>0.0077</td>
</tr>
</tbody>
</table>

CHISQ = test statistic; DF = degrees of freedom = nQ of populations - 1; P = probability of observed test statistic.

Table 9.4. Kruskal-Wallis test for comparing the fruiting phenology between eight sympatric species.

<table>
<thead>
<tr>
<th>SPECIES (Site)</th>
<th>CHISQ</th>
<th>DF</th>
<th>P&gt;CHISQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protium giganteum (Sml), Protium guianense (Sml), Protium nitidifolium (Sml), Protium paniculatum (Sml), Protium polybotryum (Sml), Protium robustum (Sml) &amp; Protium tenuifolium (Sml)</td>
<td>45.34</td>
<td>7</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

CHISQ = test statistic; DF = degrees of freedom = nQ of populations - 1; P = probability of observed test statistic.
Table 9.5. Kruskal-Wallis test for comparing the fruiting phenology between ten sympatric species.

<table>
<thead>
<tr>
<th>SPECIES (Site)</th>
<th>CHISQ</th>
<th>DF</th>
<th>P&gt;CHISQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protium alstonii (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium cuneatum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium decandrum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium nitidifolium (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium opacum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium pallidum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium Paniculatum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium sagotianum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium strumosum (Iba),</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protium trifoliolatum (Iba),</td>
<td>20.53</td>
<td>9</td>
<td>0.0149</td>
</tr>
</tbody>
</table>

CHISQ = test statistic; DF = degrees of freedom = nQ of populations - 1; P = probability of observed test statistic.

The analysis of various species of Protium in three different forests is given in Tables 9.3, 9.4 and 9.5. All three tests were significant, meaning that the congeneric species had different fruiting phenologies.

9.3. ALLOPATRIC SPECIES

In this Section the Wilcoxon’s method is used to test the null hypothesis that there is no difference between the fruiting phenologies of allopatric congeners. The results are listed in Table 9.6. It has been assumed by various naturalists (for example, Snow 1966, 1971) that species of trees belonging to the same genus and occurring at different localities of an ecosystem would not compete with one another for dispersers. This leads to the assumption their fruiting peaks would be less distinct from one another than expected for sympatric congeners. To test the
fruiting similarity between allopatic congeners, the following pairs of congeneric species were selected.

Table 9.6. Wilcoxon test for comparing the fruiting phenology between two allopatic species.

<table>
<thead>
<tr>
<th>SPECIES PAIRS (Site)</th>
<th>Z</th>
<th>P &gt; Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tapirira sp. nov.&amp; Tapirira peckoltiana</td>
<td>0.0492</td>
<td>0.9607</td>
</tr>
<tr>
<td>Thyrsodium guianense &amp; Thyrsodium spruceanum</td>
<td>0.4049</td>
<td>0.6856</td>
</tr>
<tr>
<td>Lecythis corrugata &amp; Lecythis lurida</td>
<td>3.1667</td>
<td>0.0015</td>
</tr>
<tr>
<td>Guarea kunthiana &amp; Guarea macrophylla</td>
<td>1.4671</td>
<td>0.1423</td>
</tr>
<tr>
<td>Qualea coerulea &amp; Qualea albiflora</td>
<td>2.2891</td>
<td>0.0221</td>
</tr>
</tbody>
</table>

Z = test statistic; P = probability of observed test statistic.

Table 9.6 shows that three out of five allopatic species pairs were likely to have similar fruiting phenologies while two out of five allopatic pairs were likely to have different fruting phenologies. By comparing this result with those five pairs of sympatric congeners (Table 9.2) one can see that at least for rain forest trees there is no general rule for fruting phenology of allopatic or sympatric congeners. Furthermore, the original assumption that sympatric congeners would tend to have segregated phenology as a measure to avoid competition for dispersers did not hold true for the species pairs investigated.
The reports in the literature about phenological character displacement between groups of closely related tropical species concern mainly non-tree species. They are Snow’s data on fruiting times of *Miconia* (Snow 1966), Stiles: data on flowering times of *Heliconia* (Stiles 1977) and Gentry’s flowering dates of bignonious lianas (Gentry 1974). In relation to small to medium size trees there are Prance and Mori’s report on flowering displacement in some Lecythidaceae species (Prance & Mori 1979) and Gottsberger’s report on the staggered flowering of six species of *Annona* (Gottsberger 1989).

The present investigation of sympatric and allopatric congeners did not give any evidence that fruiting phenology would be more spread among sympatric than among allopatric species. According to results on Table 9.1 not enough evidence exists to reject the hypothesis that each one of a congeneric sympatric species pair differs from the other in fruiting phenology.

It remains to be investigated whether the number of species being compared could affect the test statistic and if so, what alternatives exist. Our results suggest that whenever a large number of species is being compared (Tables 9.3 to 9.5) fruiting phenologies seem to differ but when only a small number of species are being considered (Tables 9.1 and 9.2) the fruiting phenologies seem to be the same.
Another point to make is that even when fruiting phenology of various sympatric congeners are similar in relation to percentages, the period of fruiting could still overlap. With relation to flowering phenology the results reported by Daly (1987) in 12 species of Protium, and by Mori and Prance (1987a) in 10 species of Eschweilera showed no difference among these congeners.

Finally there seems to be more reports on flowering time displacement among non-tree than among tree species. This suggests that the actual size of an individual could be related to the staggering or lack of staggering in flowering and fruiting phenologies. Large trees seem to have a more prolonged flowering and fruiting time than smaller ones, since each branch may function independently, thus allowing more flowering and fruiting overlap among congener species.
CHAPTER 10. RESULTS OF THE SOIL STUDY

10.1. INTRODUCTION

As mentioned in Chapter 2 Section 2.5, the soil studies conducted previously in the Jari basin covered only the areas of plantation forest. The only known exception was the study of plant nutrient by Russell (1983) which included a sample from one soil pit under primary forest. The present study investigated the soils found in the eight forests where the phenological observations took place.

10.2. PROPERTIES OF THE JARI SOILS

10.2.1. Soil Texture

The soils of Jari show a wide variation in texture, ranging from the almost pure quartz sands to heavy clay soils. Soil texture was found to be correlated with landscape features. The sandy soils occur in the slightly undulating alluvial plains SW of Monte Dourado, and consist of sediments of the Tertiary Barreiras Formation. Clay soils occur on the various 135-200m terraces such as are found at the Monte Dourado airport and across the river from Munguba (Felipe hills), which are Plio-Pleistocene sediments. A whole range of soils of intermediate texture fill the gaps between the table-top hills and the sandy soils of the alluvial valleys. The most fertile and best textured soils of the ‘terra firme’ forests are the loams of the planation
surfaces of the upper Jari, at the Ecological Station (IBAMA), made by Paleozoic sediments. The floodplain 'várzea' have clay to silty-clay soils which are much richer in nutrients than any of the 'terra-firme' soils studied. A serpentine of ferric sandy-clay-loam can sometimes be found among the yellow podzols found in the slightly undulating plain surfaces. Ant gardens were observed in this soil type.

Because tropical soil horizons are not normally distinct, the samples were collected according to any visible layers. In general, layer 'A' was collected at 15 cm and layer 'B' at 45-60 cm. The 'C' layer was sampled only where it was apparent in the profile and was normally collected between 70 and 100 cm. Table 10.1 shows the major soil textures and the average particle size of the soils studied.

Table 10.1. Texture classes and particle sizes of the Jari soils under primary forest

<table>
<thead>
<tr>
<th>FOREST TEXTURE CODE</th>
<th>A B C</th>
<th>A B C</th>
<th>A B C</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANG</td>
<td>% SILT</td>
<td>% CLAY</td>
<td>% SAND</td>
</tr>
<tr>
<td>Loamy-sand Sandy-loam</td>
<td>03 02 02</td>
<td>11 24 19</td>
<td>87 74 79</td>
</tr>
<tr>
<td>QUA</td>
<td>02 00 00</td>
<td>09 13 21</td>
<td>89 87 79</td>
</tr>
<tr>
<td>Loamy-sand Sandy-loam</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DOU</td>
<td>00 17 04</td>
<td>18 20 23</td>
<td>82 63 73</td>
</tr>
<tr>
<td>Sandy-loam</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SML</td>
<td>08 04 12</td>
<td>19 24 20</td>
<td>73 72 69</td>
</tr>
<tr>
<td>Sandy-clay-loam</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAC</td>
<td>05 06  -</td>
<td>57 68  -</td>
<td>38 26  -</td>
</tr>
<tr>
<td>Clay</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FEL</td>
<td>16 07  -</td>
<td>48 63  -</td>
<td>36 29  -</td>
</tr>
<tr>
<td>Clay</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ITA*</td>
<td>21  -</td>
<td>61  -</td>
<td>18  -</td>
</tr>
<tr>
<td>Silty-clay</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IBA</td>
<td>08 19  -</td>
<td>21 25  -</td>
<td>71 56  -</td>
</tr>
<tr>
<td>Sandy-clay-loam</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandy-loam</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

note: * Flood plain forest
10.2.2. Soil pH

As shown in Table 10.2 the Jari soils are very acidic, with pH ranging from 4.0 to 4.7 for the top soil. This table also shows pH values in relation to the three horizons.

Table 10.2. pH of the Jari soils under primary forest

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANGELIM</td>
<td>4.2</td>
<td>4.5</td>
<td>4.5</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>4.3</td>
<td>4.4</td>
<td>4.6</td>
</tr>
<tr>
<td>MT.DOURADO</td>
<td>4.4</td>
<td>4.2</td>
<td>4.8</td>
</tr>
<tr>
<td>S.MILITAO</td>
<td>4.0</td>
<td>4.4</td>
<td>4.7</td>
</tr>
<tr>
<td>PACANARI</td>
<td>4.2</td>
<td>4.5</td>
<td>-</td>
</tr>
<tr>
<td>FELIPE</td>
<td>4.7</td>
<td>4.9</td>
<td>-</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>4.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>IBAMA</td>
<td>4.7</td>
<td>4.7</td>
<td>-</td>
</tr>
</tbody>
</table>

10.2.3. Soil Organic Content

The organic content of the Jari soils, calculated by the method of loss on ignition, are summarized in Table 10.3. This table allows one to visualize the decrease of organic content with the increase of soil depth. The first four sandy type soils had a distinctly lower organic content than the last four clay ones.
Table 10.3. Soil type and percentage of organic content in the Jari soils under primary forest.

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>SOIL TYPE</th>
<th>LAYERS:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>ANGELIM</td>
<td>Loamy-sand</td>
<td>4.3</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>Loamy-sand</td>
<td>8.0</td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>Sandy-loam</td>
<td>5.7</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>Sandy-clay-loam</td>
<td>5.0</td>
</tr>
<tr>
<td>PACANARI</td>
<td>Clay</td>
<td>16.6</td>
</tr>
<tr>
<td>FELIPE</td>
<td>Clay</td>
<td>22.2</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>Silty-clay</td>
<td>17.4</td>
</tr>
<tr>
<td>IBAMA</td>
<td>Sandy-clay-loam</td>
<td>14.4</td>
</tr>
</tbody>
</table>

10.2.4. **Nitrogen**

The values of total nitrogen obtained indirectly by the Kjeldahl method is summarized in Table 10.4. This method is based on the conversion of organic nitrogen to ammonia. The nitrogen content found in the top soil of the eight forests studied varied from as low as .09 meq/100g in the sandy soils of Angelim forest to .34 meq/100g in the heavy clay soils of Felipe. However there was no clear correlation between soil texture and nitrogen content. The amount of nitrogen was found to diminish with soil depth (Table 10.4)

*The data for this soil layer is clearly an outlier from what was expected. Samples of charcoal were found within this layer suggesting that it could have been top soil at some time in the past.*
Table 10.4. Total Nitrogen of the Jari soils under primary forest (meq/100g Kjeldahl method).

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>LAYERS:</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>ANGELIM</td>
<td>.09</td>
<td>.06</td>
<td>.03</td>
<td></td>
</tr>
<tr>
<td>QUARUBA</td>
<td>.34</td>
<td>.27</td>
<td>.10</td>
<td></td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>.13</td>
<td>.13</td>
<td>.07</td>
<td></td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>.20</td>
<td>.01</td>
<td>.04</td>
<td></td>
</tr>
<tr>
<td>PACANARI</td>
<td>.33</td>
<td>.18</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>FELIPE</td>
<td>.34</td>
<td>.21</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>.23</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>IBAMA</td>
<td>.29</td>
<td>.22</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

10.2.5. Phosphorus

The results of the present study showed that only two of the eight forest sites studied had a phosphorus fraction higher than 50 per cent of of the total organic content. In the Jari soils studied, the available phosphorus was only 3 - 50 percent of the total amount.

Table 10.5 contrasts the total and the extractable forms of phosphorus. The results for each soil layer were kept distinct to show the influence of soil depth on phosphorus content. One can see that the IBAMA forest, which had the highest amount of organic P showed the least amount of it in extractable forms. This can be explained by the high levels of iron found in this soil as shown through visible iron pellets and smaller particles.
Table 10.5. Occurrence of Phosphorus in Jari soils under primary forests in meq./100 g of soil (TP = total P, EP = exchangeable P;).

<table>
<thead>
<tr>
<th>FORESTS LAYERS:</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TP</td>
<td>EP</td>
<td>TP</td>
</tr>
<tr>
<td>ANGELIM</td>
<td>7.1</td>
<td>2.9</td>
<td>8.5</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>8.9</td>
<td>6.0</td>
<td>7.4</td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>10.0</td>
<td>5.3</td>
<td>10.7</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>42.6</td>
<td>14.1</td>
<td>34.3</td>
</tr>
<tr>
<td>PACANARI</td>
<td>39.5</td>
<td>5.3</td>
<td>32.8</td>
</tr>
<tr>
<td>FELIPE</td>
<td>26.0</td>
<td>4.6</td>
<td>20.2</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>79.8</td>
<td>22.1</td>
<td>-</td>
</tr>
<tr>
<td>IBAMA</td>
<td>68.6</td>
<td>2.0</td>
<td>39.5</td>
</tr>
</tbody>
</table>

10.2.6. Ca, Mg, K, Na

The values for the exchangeable bases are summarized in Table 10.6.

Table 10.6. Exchangeable bases of the Jari soils under primary forest.

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>SOIL LAYERS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A Ca Mg K Na * B Ca Mg K Na * C Ca Mg K Na</td>
</tr>
<tr>
<td>ANGELIM</td>
<td>.1 .3 .2 .1 .1 .2 .1 .2 .1 .1 .1 .1</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>.2 .1 .1 .2 .2 .1 .1 .2 .1 .1 .0 .1</td>
</tr>
<tr>
<td>M. DOURADO</td>
<td>.1 .1 .2 .2 .2 .1 .2 .1 .2 .1 .1 .1</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>.3 .3 .1 .2 .1 .2 .1 .3 .2 .1 .1 .1</td>
</tr>
<tr>
<td>PACANARI</td>
<td>.4 .3 .4 .1 .2 .2 .3 .1 - - - -</td>
</tr>
<tr>
<td>FELIPE</td>
<td>.2 .3 .3 .2 .2 .3 .2 .2 - - - -</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>2.1 .4 .6 .2 - - - - - - - -</td>
</tr>
<tr>
<td>IBAMA</td>
<td>.2 .2 .2 .2 .2 .2 .1 .2 - - - -</td>
</tr>
</tbody>
</table>

10.2.7. Cation Exchange Capacity (CEC)

Table 10.7. shows that the Jari soils examined had very low CEC, mostly below 4 meq/100 g.
Table 10.7. Cation exchange capacity (CEC) of the Jari soils under primary forest (meq./100g of soil).

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>SOIL LAYERS:</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANGELIM</td>
<td>3.1</td>
<td>2.3</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>QUARUBA</td>
<td>6.3</td>
<td>3.5</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>4.9</td>
<td>5.0</td>
<td>3.4</td>
<td></td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>8.3</td>
<td>4.6</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>PACANARI</td>
<td>12.9</td>
<td>7.1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>FELIPE</td>
<td>17.2</td>
<td>7.2</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>47.8</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>IBAMA</td>
<td>9.8</td>
<td>6.8</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

The values for CEC shown in Table 2.9 are slightly different in soils of high aluminium content and low pH, due to the fact that the acidic environment allows a high amount of extractable aluminium ions. To calculate the value of CEC as it occurs in field conditions (Effective CEC), we use the following formula:

\[
\text{Ef. CEC} = \left( \frac{\text{Total Ex. Bases}}{\text{Total Ex. Bases} + \text{Al}^{3+}} \right) \times 100
\]

The Effective CEC, that is, the field value given in Table 10.8. One can see that the Ef. CEC is much higher than the CEC shown in Table 10.7. The same table also shows the pH and the total aluminium content of the various soils studied. These results confirm what was indicated above about the effect of pH on available aluminium. Because aluminium is not a very important plant nutrient, the regular CEC is a better estimate of the soil’s nutrient status.
Table 10.8. pH, Aluminium and the effective cation exchange capacity (meq./100g soil) of the Jari soils under primary forest.

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>pH</th>
<th>T. Al(mg/g)</th>
<th>SOIL LAYERS</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANGELIM</td>
<td>4.2</td>
<td>17</td>
<td>43.3</td>
<td>40.1</td>
<td>46.6</td>
<td></td>
</tr>
<tr>
<td>QUARUBA</td>
<td>4.3</td>
<td>26</td>
<td>35.0</td>
<td>33.6</td>
<td>45.8</td>
<td></td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>4.4</td>
<td>25</td>
<td>26.8</td>
<td>33.9</td>
<td>29.4</td>
<td></td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>4.0</td>
<td>41</td>
<td>21.0</td>
<td>24.2</td>
<td>31.8</td>
<td></td>
</tr>
<tr>
<td>PACANARI</td>
<td>4.3</td>
<td>132</td>
<td>22.6</td>
<td>22.3</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>FELIPE</td>
<td>4.7</td>
<td>172</td>
<td>30.5</td>
<td>71.8</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>4.0</td>
<td>106</td>
<td>24.2</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>IBAMA</td>
<td>4.7</td>
<td>83</td>
<td>59.3</td>
<td>66.5</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

10.2.8. Base Saturation Percentage

The percentage of base saturation is calculated by the following formula:

\[
\text{Base Saturation %} = \frac{\text{Total Exchangeable Bases}}{\text{CEC (Ammonium Acetate pH 7)}} \times 100
\]

The results of base saturation percentage for the Jari soils are given in Table 10.9.

Table 10.9. Base saturation percentage of the Jari soils under primary forest (meq./100 g soil).

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANGELIM</td>
<td>20.5</td>
<td>24.4</td>
<td>30.3</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>16.7</td>
<td>18.1</td>
<td>18.1</td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>10.8</td>
<td>13.6</td>
<td>14.7</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>9.6</td>
<td>14.4</td>
<td>23.3</td>
</tr>
<tr>
<td>PACANARI</td>
<td>8.5</td>
<td>18.6</td>
<td>-</td>
</tr>
<tr>
<td>FELIPE</td>
<td>5.3</td>
<td>10.2</td>
<td>-</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>5.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>IBAMA</td>
<td>7.9</td>
<td>12.7</td>
<td>-</td>
</tr>
</tbody>
</table>
10.2.9. Aluminium

Aluminium is a major element in the Amazon soils, where it is commonly found in the extractable form due to the low pH of these soils. The Brazilian system of soil classification utilizes the adjective 'alic' to those soil types with high aluminium content. Almost all the soils of Jari have extremely high amounts of aluminium (Table 2.11). A contrast between the total and the extractable aluminium can also be observed in the same table.

Table 10.10. Amounts of total and extractable Aluminium of the Jari soils under primary forest (T.Al mg/g; Ex.Al meq./100g).

<table>
<thead>
<tr>
<th>FORESTS</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>T.Al</td>
<td>Ex.Al</td>
<td>T.Al</td>
</tr>
<tr>
<td>ANGELIM</td>
<td>17</td>
<td>0.8</td>
<td>36</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>26</td>
<td>1.9</td>
<td>36</td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>25</td>
<td>1.5</td>
<td>27</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>41</td>
<td>3.0</td>
<td>50</td>
</tr>
<tr>
<td>PACANARI</td>
<td>132</td>
<td>3.6</td>
<td>158</td>
</tr>
<tr>
<td>FELIPE</td>
<td>172</td>
<td>2.1</td>
<td>260</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>106</td>
<td>7.5</td>
<td>-</td>
</tr>
<tr>
<td>IBAMA</td>
<td>83</td>
<td>1.0</td>
<td>97</td>
</tr>
</tbody>
</table>

10.3. SOIL CLASSIFICATION

Table 10.11 below gives the major soil types found under the natural forests of Jari, according to the Brazilian soil classification system.
Table 10.11. Major soils types found at Jari under primary forest (Brazilian classification system).

<table>
<thead>
<tr>
<th>FOREST</th>
<th>SOIL TYPES</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANGELIM</td>
<td>Alic red-yellow latosol, alic yellow podzol</td>
</tr>
<tr>
<td>QUARUBA</td>
<td>Alic yellow latosol with podzolic A</td>
</tr>
<tr>
<td>MT. DOURADO</td>
<td>Alic yellow podzol, quartz sands</td>
</tr>
<tr>
<td>S. MILITAO</td>
<td>Alic red-yellow latosol</td>
</tr>
<tr>
<td>PACANARI</td>
<td>Alic concretionary latosol</td>
</tr>
<tr>
<td>FELIPE</td>
<td>Alic yellow latosol</td>
</tr>
<tr>
<td>ITAPEUARA</td>
<td>Eutrophic humic 'glei'</td>
</tr>
<tr>
<td>IBAMA</td>
<td>Eutrophic structured 'terra roxa'</td>
</tr>
</tbody>
</table>

10.4. COMPARISON BETWEEN THE JARI AND THE AMAZON SOILS

The most commonly occurring soil type in the Amazon is the Latosol (Brazilian system), or oxisol (U.S.A system), or even ferrasol (FAO system) (Falesi 1976, Cochrane 1984). These soils vary in the amount of and type of clay and their physical properties are considered satisfactory (Falesi 1976). Their chemical properties are very poor, they have low pH levels, poor ion exchange capacity, poor total bases and high aluminium levels (Cochrane 1984, Lathwell and Grove 1986). This was also the most common order found at Jari.

The second most commonly occurring soil type is the red-yellow podzolics (Brazilian system) also called ultisol (U.S.A. system), and orthic acrisols (FAO system). These
soils have a low supply of total bases, low CEC and are highly acid throughout the profile. They occur at Jari but were not found among the ones sampled under primary forest.

The third type is the tropical podzol (Brazilian system) or spodosol (U.S.A. system), or giant podzol (FAO system), which are derived from coarse sandy materials. The most extensive area where this soil occurs is the headwaters of Rio Negro, where a special kind of non-forest vegetation called campina is found. In Jari this soil type was found in alluvial valleys, under dry open forests.

Table 10.12. Comparison of selected fertility patterns of Jari under primary forest and other Amazon 'terra firme' soils (data on Amazon soils from Cochrane and Sanchez, 1982)

<table>
<thead>
<tr>
<th>Parameter and range</th>
<th>% Amazon</th>
<th>Range in Jari soils</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil pH</td>
<td>81 &lt; 5.3</td>
<td>40 - 4.9</td>
</tr>
<tr>
<td></td>
<td>19 5.3-7.3</td>
<td></td>
</tr>
<tr>
<td>% Organic Matter</td>
<td>9 &gt; 1.5</td>
<td>3.7 - 21.6</td>
</tr>
<tr>
<td></td>
<td>74 1.5-4.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>17 &gt; 4.5</td>
<td></td>
</tr>
<tr>
<td>% Aluminium Sat.</td>
<td>17 0-10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8 10-40</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16 40-70</td>
<td></td>
</tr>
<tr>
<td></td>
<td>59 &gt; 70</td>
<td></td>
</tr>
<tr>
<td>Exch.Ca (meq/100g)</td>
<td>46 &gt; 0.4</td>
<td>0.1 - 0.4</td>
</tr>
<tr>
<td></td>
<td>33 0.4-4.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>21 &gt; 4.0</td>
<td></td>
</tr>
<tr>
<td>Exch.Mg (meq/100g)</td>
<td>38 &gt; 0.2</td>
<td>0.1 - 0.3</td>
</tr>
<tr>
<td></td>
<td>38 0.2-0.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23 &gt; 0.8</td>
<td></td>
</tr>
<tr>
<td>Exch.K (meq/100g)</td>
<td>62 &gt; 0.15</td>
<td>0.1 - 0.4</td>
</tr>
<tr>
<td></td>
<td>24 0.15-0.30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>15 &gt; 0.30</td>
<td></td>
</tr>
<tr>
<td>ECEC (meq/100g)</td>
<td>17 &lt; 4</td>
<td>3.1 - 17.2</td>
</tr>
<tr>
<td></td>
<td>49 4-8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>34 &gt; 8</td>
<td></td>
</tr>
<tr>
<td>Avail. P (ppm)</td>
<td>57 &lt; 3</td>
<td>1.0 - 14.1</td>
</tr>
<tr>
<td></td>
<td>33 3-7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10 &gt; 7</td>
<td></td>
</tr>
</tbody>
</table>
10.5. DOES SOIL AFFECT PHENOLOGY?

In Chapter 6 the correlation coefficients were calculated for some important soil variables of each forest community studied with the variables maximum flowering percentage and maximum fruiting percentage. The result was that no correlation was found among such variables. Such result can be inferred by the simple inspection of the data on the month of peak flowering or fruiting (Table 6.2). The only correlation found was between percentage of sand in soil with percentage of organic matter and vice versa (Table 6.3).
CHAPTER 11. SUMMARY AND DISCUSSION

11.1. MODELS OF SPECIES PHENOLOGY

In Chapter 5 the phenology of each tree species was described individually, and classified according to their phenological model (Tables 5.2-5.16). The definition of these models was the subject of Chapter 8.

As far as vegetative phenology of individual species of trees is concerned, this study showed that the trees found in the seasonal forests of Jari can be semideciduous, deciduous or evergreen. In the Jari river basin as in other areas that show seasonality most trees are deciduous. However, even in seasonal forests the proportion of deciduous or evergreen species can be an important ecological indicator of the forest.

11.2. PATTERNS OF COMMUNITY PHENOLOGY

Like many other phenological studies in neotropical forests (e.g. Frankie et al. 1974a, Monasterio & Sarmiento 1976, etc.), the forests of Jari showed very clear seasonal patterns of leaf shedding as well as of flowering and fruiting. The phenology literature has documented that in the seasonal neotropics herbs and shrubs tended to flower during the rainy season while most tree species tended to flower during the dry season (Croat 1969, Monasterio & Sarmiento 1976, Frankie et al. 1974a,b).
Furthermore many phenological studies have pointed out the occurrence of staggered flowering peaks in different tree species interpreting this as a mechanism to avoid competition between species for the same pollen vectors (Heithaus 1974, Frankie 1975, Stiles 1977, 1978).

One could speculate that because of the role of fruits in the food chain, fruiting should be evenly distributed throughout the year. However, all studies in tropical fruiting phenologies report seasonality, which occurs to a greater extent in forests with distinct wet and dry seasons. It follows that food scarcity is a normal occurrence in seasonal forests (Howe 1984) and that food abundance may have a strong effect on whether a particular vertebrate is a predator or a dispersal agent (Janzen 1971).

Leaf fall was found to occur throughout the year but at much greater intensity during the dry season. Year to year variation occurred in all forest sites studied. No significant variation was observed between sites at any particular point in time. The more pronounced dry season of 1988/89 affected equally all the forests studied, which had a much reduced flowering peak than the preceding and following years.
11.3. FACTORS THAT INFLUENCE PHENOLOGY

There has been much debate concerning the exogenous versus endogenous control of flowering and fruiting in tropical trees. Many authors have speculated on which are the cues that trigger flowering in tropical trees. Those which attribute flowering to environmental causes have suggested rainfall (Augspurger 1983) or photoperiod (Alvim & Alvim 1978), while others attribute flowering to internal mechanisms (Falcão & Lleras 1980, 1981, 1982, 1983, Falcão et al. 1981).

To understand flowering and fruiting phenology a distinction must be made between proximate mechanisms and the ultimate ones that control these processes. In the case of flowering an environmentally dependant physiological mechanism such as drought stress may be the proximate cause of phenology but not the selective force for it.

The role of the environment in tropical phenology is very difficult to assess because it can be either direct by affecting the plant's ability to produce flowers or indirect by affecting pollen vectors (Rathcke & Lacey 1985). Furthermore, even the direct environmental effect is not easy to define. Perhaps one of the best example is the difficulty in separating between different tree niches (canopies) within a forest community (Frankie et al. 1974, Pires 1984). The fact that every community studied showed a flowering peak during the dry season is evidence that
flowering could be caused by the hydration resulting from the reduction in transpiration following leaf shedding. Each individual tree probably has its own optimum hydric balance for flowering. A too mild or too harsh dry season could lessen the proportion of flowering among trees of a population.

This study assumed that the climate of all the forests studied was constant since they were all located within the same micro-region where the distance between the two farthest forests was less than one degree of latitude. Thus soil and its components were the only significant environmental factor that could separate the forest communities studied (Figure 6.1).

The ecological distances between the eight forest communities studied, illustrated in Figure 6.1, was calculated by the cluster analysis of ecologically important variables. Although as a result of the cluster analysis the eight sites were placed into four clusters (Figure 6.1), seven sites showed very small distances from one another. Only the Ibama forest showed a substantial ecological distance from the remaining forests, suggesting that such forest community could belong to the floristic province of Guiana rather than to the floristic province of the Amazon.

To study the influence of the environment on the success of flowering and fruiting phenologies, regression analysis was
carried out between maximum flowering percentage and maximum fruiting percentage and ecologically important soil variables. No correlation was found between them (Chapter 6).

Figures 6.14 to 6.17 suggest that there are very little difference in the phenology phases of the eight forest communities studied. This result agrees with those of a similar study in India, which showed no difference in the phenology of six forest communities of different altitudes from the same micro-region (Ralhan et al. 1985).

The phenology of the eight forest communities studied was not modified by any of the environmental variables tested (Chapter 6). However, the phenology of trees from the Jari micro-region as a whole showed strong correlation with rainfall (Chapter 7).

The fact that only some 20 per cent of the Jari trees flowered even at the peak of flowering activity can be considered evidence that genetic polymorphism of genes controlling anthesis in trees is the ultimate cause of flowering phenology. The environmental variables such as rainfall and photoperiod can thus be interpreted as proximate causes of flowering phenology.
11.4. PHENOLOGY OF SYMPATRIC AND ALLOPATRIC CONGENERS

One of the major problems in the study of tropical rain forest ecology is to explain the origin and coexistence of similar and closely allied species in such forests. Such fact apparently contradicts the theory that morphologically allied species of plants could not have survived in the same habitat since they would compete for resources and such competition would lead to their extinction on a local scale (Darwin 1859, Mayr 1944).

Some tropical evolutionary ecologists explain the occurrence of closely allied species in the same forest by arguing that their characters have evolved to avoid competition by permitting resource partitioning (Levins 1968), resulting in what has became known as ‘character displacement’. Another explanation is that they occupy different niches of the forest such as upper and lower canopies as another way to avoid competition for resources and gene exchange. Flowering phenology has also been pointed out as a type of isolation mechanism to reduce interspecific gene flow and to avoid competition for resources (Levin & Anderson 1970). Closely related species which share the same pollinator could evolve phenological character displacement and thus flower at different times. But when the pollinators shared are rare or widely dispersed then there may be an advantage for them to flower together and provide a larger floral display to attract
pollinators. In this case a genetic isolating mechanism must already exist between the species.

When species of the same genus occur at different localities of an ecosystem the selection to avoid competition for pollinators and against interspecific gene flow is supposedly less than that found in sympatric congeners. To test the fruiting similarity between allopatric congeners, five pairs of congeneric species were studied. The present investigation showed that at least for large rain forest trees there is no clear indication of flowering staggering among sympatric species or more flowering overlap among allopatric species, as found to occur with non-trees and smaller trees. The flowering peak displayed by most of the tree species observed during our study occurred at the end of the dry season and beginning of the wet season. The fruiting peak occurred during the wet season, and was usually more extended than the flowering peak. It is obvious that there are not enough dry and wet seasons in a year to accommodate the many different peaks required for staggering to take place among sympatric congeners. This is even more so for trees since the duration of the flowering and fruiting phases tend to be correlated with organism size. Indeed, when the species involved share pollinators and/or dispersers there may be an advantage in simultaneous flowering or fruiting.

Other investigations in tropical phenology have found similar results. A study by Koptur (1984) with several
Inga species in Costa Rica revealed that although many species bloomed simultaneously, none were cross-compatible. Furthermore, Koptur (1984) found that pollination within a species was only possible when pollen from other trees was used and that the pollination success was twice as great when pollen was obtained from a tree located at 1 Km distance than when the pollen donor was at 500 m from the receptor.

Another study carried out in a seasonal forest in French Guiana by Mori and Prance (1987a) found that 25 out of 26 species of Lecythidaceae trees flowered either in the dry season or during the transition from the dry to the wet season. A third study by Sabatier (1985), also in French Guiana, found the same flowering pattern for 10 species of Lecythidaceae occurring at another area. These results suggest that tropical trees rely on other reproductive isolating mechanisms rather than flowering and fruiting phenology (Rathcke & Lacey 1985, Mori & Prance 1987a).

11.5. FURTHER WORK

The flowering and fruiting phenologies of tropical trees as provided in the present already allow not only inferences on the general aspects of tropical phenology but also to estimate the amount of genetic variability of the species studied. The present thesis used observational data to answer to a 'how-type' question and interpreted such data to explain the facts encountered in light of current
ecological methodology. However, for a fuller understanding of phenology there is also a need to study many of the 'why-type' questions. These last have to do with pollination, fertilization, seed production and seedling establishment. The following research activities are proposed to further the present study.

(1) To select a restricted number of tree species for further study;

(2) To locate additional natural populations of the chosen species;

(3) Investigate the basic phenological differences between populations by means of cytological techniques;

(4) Investigate possible isolating mechanisms through species-specific chemical signs in pollen and stigma;

(5) Investigate the possibility of agamospermy in cross pollinated species;

(6) Relate the above to the ecology of the species;

(7) Create a system for adequate data storage and retrieval;
REFERENCES


Newton, P. N., (1988). The structure and phenology of a moist deciduous forest in Central Indian Highlands. Vegetatio, 75,3-16.


CNPq/INPA, Manaus.


APPENDIX I. LIST OF VOUCHER MATERIALS AND MARKED TREES.

The information below is organized by plant family, species code and name, nQ of individuals per species, vernacular name of species, forest sites, voucher collections and tree number. Collections following the vernacular name refer to other trees of the same species collected at Jari. Unless otherwise specified all plant collections are deposited at the herbarium of the Royal Botanic Gardens, Kew.

Abbreviations and symbols used:
* tree died during the course of the experiment.

Collector names:
MJP = M.J.Pires et al.
C = M.A.Conceição

Forest sites:
SM = São Militão, PA = Pacanari AN = Angelim, QU = Quaruba,
FE = Felipe, MD = Monte Dourado, IT = Itapeuara, IB = Ibama.

Herbaria:
JARI = Companhia Florestal Monte Dourado, PA
NY = New York Botanical Garden

Status of Collection:
st = sterile
fl = flowering
fr = fruiting
se = seeds
s1 = seedling

Collector names:
MJP = M.J.Pires et al.
C = M.A.Conceição

ANACARDIACEAE n= 75
080 Anacardium giganteum Hancock ex Engler; n= 16
(Cajú-açu)
SM MJP-1880st,-1970f1,-2055se,-2290st
(1288,1162,1162,1387).
Trees:287,1127,1162,1181,1288,1382,1387,1500
AN MJP-2067st,-2066st,(301,376);Trees:301,376,643
QU MJP-1925f1(47);Trees:47,127,136*,153
MD MJP-1899f1(450);Tree:450

082 Anacardium spruceanum Bentham; n= 2
(Cajuí)
FE MJP-2184st,-2185st(110,893); Trees:110,893

050 Astronium obliquum Griseb; n= 16
(Aroeira)
SM MJP-2153st(667), C-142st(667); Tree:667
PA MJP-2357st(522); Tree:522
A N MJP-2075st(100); Trees: 100, 141, 179, 431, 472, 566, 699, 800, 835, 950
QU MJP-2081st(162), C-95st(224); Trees: 162, 224
IT MJP-2311st(684), C-30f1(684); Trees: 656, 684

334 Spondias mombin L.; n= 1
(Taperebá)
SM MJP-1989st(700); Tree: 700

335 Tapirira guianensis Aublet; n= 11
(Tatapiririca) MJP-656
SM MJP-2154st(974); Tree: 974
AN MJP-2295st(573); Tree: 573
QU MJP-1873f1(680); Trees: 267, 567, 680
MD MJP-1903f1(485); Tree: 485
IT MJP-2318st(790); Tree: 790
IB MJP-1838f1(07); Trees: 01, 07, 168, 540

310 Tapirira peckoltiana Engler; n= 4
(Tatapiririca peluda) MJP-726
IB MJP-1871f1(709); Trees: 709, 721, 885, 959

307 Tapirira sp. nov.; n= 5
(Tatapiririca vermelha)
FE MJP-1802f1+fr(282); Trees: 191, 282, 673, 753, 916

031 Thyrsodium guianense Sagot ex March.; n= 14
(Amapararé) MJP-1427, 1873 (JARI)
FE MJP-1854f1(658); Trees: 336, 537, 586, 588, 604, 659
MD MJP-1898f1(460), C-199 (560);
Trees: 151, 373, 460, 560, 835, 838, 872, 910

030 Thyrsodium spruceanum Bentham; n= 6
(Amaparana) MJP-1921 (JARI)
IB MJP-1917st(236); Trees: 236, 129, 839, 809, 887, 879

BOMBACACEAE n= 23

549 Bombacopsis nervosa (Uitt.) A. Robyns; n= 1
(Mamorana da t.f)
SM MJP-2263st(834); Tree: 834.

711 Eriotheca crassa (Uitt.) A. Robyns; n= 2
PA MJP-2358st(510); Tree: 510
IB MJP-2344st(772); Tree: 772

210 Eriotheca globosa (Aublet) A. Robyns; n= 3
(Mamorana)
PA MJP-2265st(300); Tree: 300;
FE MJP-2186st(242); Trees: 242, 628

417 Eriotheca surinamensis (Uitt.) A. Robyns; n= 8
(Mamorana da caatinga) MJP-2404f1
AN MJP-2065st(125); Trees: 125, 485
QU MJP-2092st, 2091st(229, 837);
Trees: 229, 837, 938, 966, 991, 996*
623 Pachira aquatica Aublet; n= 2  
(Mamorana casca dura)  
IT MJP-2039f1,-2355a&bfr(159); Trees:110,159

243 Pseudobombax munguba (Mart.& Zucc.) Dugand; n= 2  
(Munguba)  
IT MJP-2319f1(328); Trees:328,588

161 Quararibea quianensis Aublet; n= 7  
(Inajarana) MJP-805 (JARI)  
IT MJP-1999f1+fr(431); Trees:311,393,431,436,461,335,509

BURSERACEAE

545 Protium alsotonii Sandw.; n= 14  
(Breu mescla)  
SM MJP-1879f1(1589); Tree:1589  
IB MJP-2380st,-1915f1,-1918f1,-1919f1,-1926f1  
(659,126,340,459,321), C-9st(351);  

746 Protium apiculatum Swart vel aff.; n= 1  
(Breu vermelho 3)  
IB C-7st(132); Tree:132

454 Protium cuneatum Swart; n= 4  
(Breu pipiranga)  
IB MJP-1872fr(767),C-19f1,-202st,-205st(570,911,726);  
Trees: 570,726,767,911

076 Protium decandrum (Aublet) Marchand; n= 4  
(Breu vermelho) MJP-1678(JARI)  
IB MJP-1870f1(182),C-8st,-33st(625,736);  
Trees:182,625*,736,732

072 Protium giganteum Engler; n= 36  
(Breu branco da folha grande)  
SM MJP-1968fr(278);  
Trees:134*,278,301,1278,412,425,433*,441*,515,534,1070,  
1073,1086,1135,1266,1386,1406,1457  
AN MJP-1910f1(263); Tree:263  
QU MJP-1848f1(314); Trees:33,198,221,284,314*,333*,339,835  
FE MJP-1885fr(912); Trees:251,290,692,746,826,912  
MD MJP-1961fr(934); Tree:934  
IT Trees:675,652

475 Protium guianense (Aublet) Marchand; n= 5  
(Breu X)  
SM MJP-2156st,-2281st,-2286st (1261,1384,217), C-11st,-  
18st(408,290); Trees:217,290,408,1261,1384

630 Protium cf. mori Daly; n= 4  
(Breu vermelho da folha grande)  
AN MJP-1867st(815); Trees:815,851  
IT MJP-2321st,-2312(855,685); Trees:685,855

306
715 Protium nitidifolium (Cuatr.) Daly; n= 10
(Breu amaparana 1) MJP-1497f1, -2099fr
SM MJP-1966 & -2284, -2288(155,1332); Trees: 155,1332
FE MJP-1883f1, -1930f1(414,407); Trees: 407,414
IT C-01st(679); Tree: 679
IB MJP-1914f1, -1920f1, -2348st(821,812,417), C=15st(654);
Trees: 254,417,654,812,821

450 Protium opacum Swart cf. subsp. rabelianum; n= 21
(Breu jatoá)
PA MJP-2359st(591); Trees: 591,608,623,1097
FE MJP-2187st(934), C- 129st,106st,107st,118st
(A-49,892,951,876,905); Trees: 49,626,876,892,905,*934,951
IT MJP-2320st(930); Trees: 930,980,989
IB MJP-2383st(467), C-12st,16st(A-345,427);
Trees: 345,382,427,467,477,604,791

070 Protium pallidum Cuatr.; n= 9
(Breu branco) MJP-1468
IB MJP-1869st(237), C-13st,20st(338,97);
Trees: 97,237,244,332,338,411,469,482,608

257 Protium paniculatum Engler; n= 12
(P. giganteum; Breu amarelo)MJP-1678f1
SM MJP-1861f1, 1878f1(1447,1597), C-147st, -148st(1537,1447);
Trees: 1353,1447,1537,1597*,1678*
FE MJP-2096fr, -1881f1(175,175), C-104st,130st,131st
(A-875,820,875); Trees: 115,485,820,875
IB MJP-1868f1,(43); Trees: 43*,207,271

451 Protium polybotryum (Turcz.) Engler subsp. polybotryum;
n= 18; (Breu vermelho do fruto roxo, breu amescla);
Beck et al.-100(NY), MJP-1862(JARI)
SM MJP-2106fr, -2157st, -2280st, -2283st, -2289st(1287,1179,
1331, 116,1435), C-143st,144st,145st,146st
(1508,1699,1024,1377);
Trees: 116,1179,1287,1331,1435,1508,1699,1024,1377
PA MJP-2361st(449); Tree: 449
IT MJP-1856f1, -2176st(704,693), C-2st,3st,4st,5st
(765,768,781,817); Trees: 704,693,768,781,765,817
IB MJP-2381st(755); Tree: 755

071 Protium robustum (Swartz) Poster; n= 5
(Breu folha grande); Beck-012(47-SM)
SM MJP-2155st(1652); Trees: 1236,1652,1670
IT MJP-1942fr(755); Trees: 755,921

074 Protium sagotianum Marchand; n= 83
(Breu preto)
MJP-1655s1; Rabelo et al.-3537(NY); MJP-1979f1
PA MJP-1949f1, -1953f1(814,297);
Trees: 3,16,217,287,297,411*,446,479,638,724,786,814,897,
907,909,1062,
AN MJP-1978f1(734); Trees: 150,169*,203,250,255,287,622,677
712,734,764,795,911,959
QU MJP-2085st, -2086st(53,45);
FE MJP-1929f1(307), C-119f1(753);
Trees: 29, 107*, 307, 345, 753, 870, 946, 998;
MD MJP-1971f1, -2102fr, -1972f1(458, 497, 705); Trees: 5, 91, 261, 418, 458, 497, 554, 703, 705, 787, 789, 875, 942, 951, 952*
IT MJP-2322st, -2323st, -1941f1(695, 788, 769);
Trees: 695, 691, 697, 748, 769, 773, 788, 852, 894, 863, 895, 894, 975, 1000, 1003
IB MJP-2378st, -2379st, -2382st (346, 639, 704); Trees: 346, 639, 704

747 Protium strumosum Daly; n= 5
(Breu vermelho do paredão)
IB MJP-2346st(A-82), C-14st, -10st, (601, 619);
Trees: 82, 345, 408, 601, 619,

579 Protium subserratum (Engl.) Engler var.; n= 2
(Breu vermelho 2)
AN MJP-2074st(789); Tree: 789
FE MJP-2188st(639); Tree: 639

453 Protium tenuifolium Engler; n= 8
(Breu pretense) MJP-1975 (NY)
SM MJP-2285st, -1892f1(180, 377);
Trees: 100, 180, 114, 377, 606, 991, 1453, 1532

748 Protium trifoliolatum Engler; n= 2
(Breu sem cheiro)
IB C-17st(210); Trees: 210, 374

712 Protium sp. nov. 1; n= 1
(Breu vermelho 3)
FE C-132st(690); Tree: 690

714 Protium sp. nov. 2 (P. aff. unifolium); n= 1
(Breu folha simples) MJP-1603fr
PA MJP-1945f1(565); Tree: 565

716 Protium sp. nov. 3; n= 3
(Breu amaparana 2)
IB MJP-2103fr(480); Trees: 308, 480, 725

073 Tetragastris altissima (Aubl.) Swartz; n= 12
(Breu manga) MJP-1436(NY)
PA MJP-1778st(1041); Trees: 375, 456, 1041, 1059, 1085, 1100
IT MJP-2324st(1010); Tree: 1010
IB MJP-2347st(242); Trees: 242, 381, 643, 748, 995

452 Tetragastris hostmannii (Engl.) Kuntze; n=30
(Breu paraense)
AN MJP-2072st, -2071st(891, 45), C-64st, 65st, 71st, 72st, 74st, 76st, 77st, 78st, 79st(59, 46, 117, 723, 662, 363, 623, 331, 298);
Trees: 45, 46, 58, 59, 73, 76, 78, 117, 177, 178, 186, 298, 331, 363, 583*, 623, 662, 723, 891
QU MJP-2079st, -2306f1(02, 215), C-87st, 88st, 89st, 90st, 91st, 92st, 93st(A-65, 15, 170, 180, 217, 380, 494);
Trees: 2, 15, 65, 170, 180, 182, 215, 217, 380, 494
069 *Tetragastris panamensis* (Engler) O’Kuntze; n= 27
(Breu areu-areu) MJP-1437; Beck-26(150-sm)
SM MJP-2282st,-1820fr,-2137st(48,1616,1616);
Trees:48,1144,1214,1234,1489,1512,1563*,1616,1671
PA MJP-2266st,2267st(173,210),C-50st(566);
Trees:173,210,468,566
FE MJP-1927fl(078),C-133st,134st(187,669); Trees:78,187,669
MD MJP-2114st(6); Tree:6
IT MJP-2325st(923); Tree:923,958,988,999,898,1012
IB Trees:252,529,745*,842

455 *Trattinickia burseraefolia* Mart.; n= 6
(Breu sucuruba branco)
AN MJP-2296st(703); Tree:703
QU MJP-1849fr(178); Tree:178
SM MJP-2287st(261); Trees:261,1587
FE MJP-2225st(271); Tree:271
IB Tree:385

749 *Trattinickia glaziiovii* Swart; n= 1
Breu paraense 2
QU C-94st(191); Tree:191

**CARYOCARACEAE**

284 *Carvocar glabrum* (Aublet) Pers.; 18
(Piúiá-rana)
SM MJP-2169st(1289); Trees:1276,1289
PA MJP-1893st(316); Tree:316
AN MJP-1906st(16); Trees:16,170*,396,541,700,829,927,997
FE MJP-2189st(293); Trees:195,293
MD MJP-1900fl(148); Tree:148
IT MJP-2326st(268); Trees:268,286
IB Trees:361,890

285 *Carvocar microcarpum* Ducke; n= 5
(Piúiá-rana da várzea)
IT MJP-1857fl,-1858fl(86,183); Trees:86,148,183,225,229

283 *Carvocar villosum* (Aublet) Pers.; n=3
(Piúiá)
SM MJP-2008st(481); Trees:448,481,1166

710 *Carvocar pallidum* A.C. Smith; n= 1
(Piquiarana 2 - estames rosa)
IT MJP-2327st(300): Trees:300

**CHRYSOBALANACEAE**

131 *Couepia ouianensis* Aublet; n=8
(Cumatê)
SM MJP-2158st(101); Trees:101,1167,1667(s.sp. guianensis)
PA MJP-2049fl(729); Trees:171,729,848 (s.sp. guianensis)
IT MJP-1745fl(663),C-29st(785); Trees:663,785
(s.sp. divaricata (Hub.) Prance
414 *Couepia joaquinae* Prance; n=4  
(Cumatê 2)  
FE Beck-37fr/(NY)(199),C-175f1,177f1,178f1,  
176f1(199,309,840,846); Trees:199,309,840,846

252 *Couepia robusta* Huber; n=1  
(Pajurá)  
FE MJP-2223st(748); Tree:748

158 *Hirtella bicornis* Mart. & Zucc. s.sp. pubescens Ducke;  
n= 35 (Farinha seca br.) MJP-1423 (NY);C-156st(1285)  
SM C-149f1,150f1,151f1,152f1,153st,154st,155st  
(200,37,45,248,238,451,516);  
Trees:45,37,200,238,248,451,516,  
PA MJP-2363st(1076),C-51st,52st,53f1,-211f1(465,715,  
1063,465); Trees:465,715,1063,1076  
AN MJP-1909f1,-2375st,-1423f1(307,222,264),  
C-57st,66st,67st,80st(264,913,879,999);  
Trees:222,264,307,879,913,999,  
QU MJP-2206st(190); Tree:190  
FE MJP-2230st,-2234(82,335); Trees:82,335  
MD MJP-2115st(814); Trees:401,462,653,723*,814*,943,918  
IT MJP-2328st(804).C-22f1,23f1,24f1,27f1,31b.f1,207f1(827,  
851,877,714,736,758);  
Trees:758,736,714,804,827,851,877,881*

700 *Hirtella eriandra* Bentham; n= 4  
(Farinha seca vermelha 2)  
SM MJP-1817f1,-1863f1 (920,221), Beck-13 (NY)(221);  
Trees:221,869,920  
MD MJP-2031fr(247); Tree:247

462 *Hirtella obidensis* Ducke; n= 9  
(Caripe vermelho)  
PA MJP-2268st(225); Tree:225  
AN MJP-2293st(103),C-58st,59st(242,409); Trees:103,242,409  
FE MJP-2191st,-2231st,-2232st,-2233st(296,99,283,334),  
C-127st(863); Trees:296,99,283,334,863

144 *Hirtella piresii* Prance; n= 9  
(Farinha seca vermelha); Rabelo-3533  
FE MJP-2192st(225),C-108f1,109st,110st,111st,112st,  
113st,120st(513,937,365,568,643,220,864;  
Trees:220,643,937,365,864,568,225,513,479

550 *Licania apetala* (E.Mey.)Fritsch; n= 4  
(Caripê da várzea, caripê matupiri)  
MD MJP-2134st,-1352f1(135,138); Trees:135,138,207  
IT MJP-2329st(623); Tree:623

701 *Licania canescens* R. Ben; n=4  
(Caripê branco 2)  
SM MJP-2277st,-2163st(1602,149); Trees:149,1602  
FE C-102st,103st(226,57); Trees: 57,226
702 **Licania egleri** Prance; n=15
(Caripê matupiri 2)
FE MJP-2228st,-2229st,-2235st,-2236st,-2193st,-2190st,-2237st
(178,284,818,903,344,500,911), C-97st,98st,99st,122st,123st,
124st,128st(861,339,579,472,455,505,574);
Trees:178,284,339,344,
455,472,500,505,574,579,818,861,903,911,
IT C-6f1(991); Tree:991

206 **Licania heteromorpha** Bentham var. heteromorpha; n=32
(Macucú) MJP-1998
SM MJP-2159st(1411); Trees:846,1111,1411,1499,1691
PA MJP-2364st(667); Trees:667
AN MJP-1996fr(624), C-55fr(35);
Trees:35,249,230,275,335,408,601,624,634,
QU MJP-1924fr(163), C-81fr(171);
Trees:19,119,139,163,171,187,278,468,499
FE MJP-2239st,-2240st,-2241st,-2243st,-2244st,-2246st
(445,448,474,581,859,731); Trees:445,448,474,581,731,859
IT MJP-1938fr(856); Trees:856,879

385 **Licania impressa** Prance; n=4
(Caripê branco)
FE MJP-1803fr,-1884fr(685,685), C-100st,101st(303,253);
Trees:253,303,685,971

089 **Licania kunthiana** Hook f.; n=8
(Caripê pintadinho)
PA C-165fr,166fr,169fr,171fr,174fr,209st
(986,1032,927,382,1033,155);
Trees:155,382,927,986,1032,1033
QU MJP-2207st(194); Tree:194
IT MJP-2331st(776); Tree:776

704 **Licania laevigata** Prance; n=9
(Macucú vermelho 2)
SM MJP-2161st(767); Tree:767
FE MJP-2238st,-2242st,-2245st,-2247st(250,477,278,919);
Trees:250,278,477,919
MD MJP-2116fr(704); Trees:227*,704,839
IT MJP-2313(687); Tree:687

508 **Licania latifolia** Benth. ex Hook.; n=3
(Macucú vermelho)
AN MJP-2068st(735); Tree:735
QU MJP-1922fr(651); Trees:651
IT MJP-2332st(843); Trees:843

085 **Licania macrophylla** Bentham; n=8
(Macucú branco, anoerá)
IT MJP-2330st(920), C-21st(803);
Trees:803,889*,920,924,952,950,964*,978

464 **Licania micrantha** Miq.; n=12
(Caripê-rana am.) MJP-141
SM MJP-2162st(604); Tree:604
AN MJP-1822fr(243), C-61st,62st,63st,69st,70st,73st,75st

311
(296,297,296,775,484,760,360); Trees:243,296,297,360,484,760,775,926
QU MJP-1923f1(503),C-96st(641); Trees:503,641
MD MJP-1973f1(870); Trees:870

591 Licania minutiflora (Sagot) Fritsch; n= 2
(Pajuru da varzea)
IT MJP-1859fr,1889st,-2342st(413,413,832); Trees:413,832

034 Licania octandra (Hoff.,ex R.& S.) Kuntze; n= 6
(Caripê seco)
PA C-170st,172st,173st,210st(665,756,847,1096)
Trees:665,756,847,1096 (s.sp. pallida)
AN C-68st(139); Tree:139 (s.sp. octandra)
QU MJP-2090st(924); Tree:924 (s.sp. octandra)

463 Licania pallida Spruce, ex Sagot; n= 13
(Caripê pintadinho 2); MJP-1956fr
SM MJP-2166st,-2274f1,-2275st,-2160st(170,249,1659,115);
Trees:115,170,249,1659
PA MJP-2058st,-2269st(273,115); Trees: 115,273,345,915
MD MJP-1739f1(90),C-162fr,163st,164fr,208st
(493,935,673,921);
Trees:90,493,673,921,935

090 Licania robusta Sagot; n= 4
(Cariperana amarela 2)
FE MJP-1882f1(287),C-121st,125st,126st(301,396,796);
Trees:287,301,396,796

709 Licania silvae Prance; n=2
(Farinha seca verme. 3)
IB MJP-2385st(848); Trees:28*,848

258 Parinari excelsa Sabine; n=17
(Parinari)
SM MJP-2180st(65); Trees:65,550,591
PA MJP-2365st(694); Trees:694
AN MJP-2292st((160); Trees:160,448,631,774,845,850
QU MJP-2208st,-2209st(249,413); Trees:249,413
MD MJP-2117st(99); Tree:99
IT MJP-2333f1(208); Trees:208,215,1017,1018

CONNARACEAE

239 Connarus perrottetii (DC.) Planchon; n= 9
(Muirassacaca)MJP-553f1
QU MJP-2080st(14); Trees:14,252,257*,470,512,662,893,897
AN MJP-2076st(720); Tree:720

HUMIRIACEAE

348 Endopleura uchi (Huber)Cuatr.;n=19
(Uchi)
SM MJP-2164st(1203); Tree:1203
PA MJP-1951f1(028); Trees:28,48,563,972
AN MJP-2077fr(656); Trees:656,729,780
FE MJP-2194st(109);Trees:67,91,109

312
MD MJP-1762fl,-1763st(132,264);
Trees:132,264,271*,291,630,636,716,757

359 **Humiria balsamifera** (Aubl.) J. St. Hil.; n= 15
(Umiri) MJP-2063f1
AN MJP-1753f1(571); Trees:532,535,551,557,562,571,572
QU MJP-2089st,-2078st(474,547); Trees:474,547*,714,865,884
902,976*,982

349 **Saccoglossis guianensis** Benth.; n= 27
(Uchi-rana) MJP-2070st(38); Trees:8,38,221,625,844
QU MJP-2088st,-2087st(31,106);
Trees:31,106,366,505,556*,647,654*,720
FE MJP-2183st(240); Trees:177,240,497,561,936,948
MD MJP-1974st(949); Trees:222,290,713,949,784,762,805
IB MJP-1785f1(24); Tree:24

259 **Vantanea parviflora** Aublet; n=26
(Parurú); MJP-1966f1
SM MJP-2278st(1414); Tree:1414
PA MJP-2366st(1088); Tree:663,686,1065,1088
AN MJP-1754st(525); Trees:27,69,67,176,366,391,525,617,714
QU MJP-2210st(44); Trees:44,598*
MD Trees:731,832,878*,899
FE MJP-2195st(451); Trees:346,451,452,457
IB MJP-2386st(669); Trees:669,955*

**LECYTHIDACEAE**

097 **Bertholletia excelsa** H. & B.; n=22
(Castanha do Pará) MJP-1969st(1122);
Trees:9,12,187,223,452,608,1122,1654
PA MJP-1959st(946); Trees:33,97,108,168,280,453,726,946
MD MJP-2118st(874); Trees:344,874
IT MJP-2334st(650); Trees:650,775,846
IB MJP-2349st(892); Trees:892

338 **Couratari guianensis** Aublet; n=12
(Taurí) MJP-1651
SM MJP-2170fr(378); Trees:378,656
AN MJP-2376st(871); Trees:871
MD MJP-1720fr(411); A:411,781,807
FE Trees:134,440,827
IT MJP-2310st(615); Tree:615
IB MJP-2387st(342); Trees:146,342

535 **Couratari oblongifolia** Ducke & Knuth; n=1
(Taurí branco) MJP-2297st(721); Tree:721

095 **Couroupita guianensis** Aublet; n= 2
(Castanha de macaco)
IT MJP-1744st(460); Trees:334,460

230 **Eschweilera amazonica** R. Knuth; n= 9
(Matá matá cí)
FE MJP-2248st,-2249st,-2250st,-2251st,-2252st(737,797,813,
933,969),C-114st(797); Trees:737,797,813,933,969
227 *Eschweilera coriacea* (A.P. DC.) Mart. ex Berg; n=25  
(Matá matá branco)  
SM MJP-2165st(1079); Trees:53,702*,1002,1079,1080,1193*,1131,1202,1617*  
PA MJP-2367st(578); Trees:518,578,596,765,865,809,956,1039  
IT MJP-2308st(544); Trees:127,373,544,629,661,760,931,966

407 *Eschweilera grandiflora* (Aublet) Sandwith; n=1  
(Matá-matá flor grande) MJP-1994f1,-1426(NY)  
FE MJP-1928f1,-1887f1(499,499); Tree:499

228 *Eschweilera obversa* (Berg.) Miers; n=8  
(matá matá castanhola) MJP-588,1388 (NY)  
QU MJP-2211st,-2212st,2213st(24,96,185),C-82fr,83fr,84fr,85st,86st(A-207,132,96,143,166); Trees:9,24,96,132,143,166,185,207

208 *Eschweilera pedicellata* (Richard) Mori; n=9  
(Matá matá rosa da t.f.)  
MJP-1420,1787;Rabelo et al.-3540(NY)  
PA MJP-1946st(507); Trees:507,761,812  
MD MJP-1895f1,-1847f1(345,122); Trees:122,345,854  
IT -2314st(797); Trees:797,848  
IB MJP-2389st(835); Tree:835

718 *Eschweilera sp. 1*; n=10  
(Matá mata branco do paredão) MJP-2370(122)  
AN MJP-2373st(856); Tree:856  
IB MJP-2350st(212),C-36st(114); Trees:114,199,212,246,262,466,490,522,928

153 *Gustavia augusta* L.; n=24  
(Geniparana) MJP-813,Beck et al.-23(NY)  
SM MJP-2141st(748); Trees:672,748,882,941,1004,1016,1228,1374  
PA MJP-2004f1(1080); Trees:10,13,181,211,325,945,1080,1092  
IT MJP-2307st(395); Trees:22,43,73,253,363,395,517,527

178 *Gustavia hexapetala* (Aublet) J.E. Smith; n=1  
(Jarana, geniparana da várzea)  
IT MJP-2309f1(527); Tree:527

181 *Lecythis corrugata* Poiteau subsp. corrugata; n=4  
(Jateréu morrão) MJP-1492 (NY)  
SM MJP-1891f1(280),C-157st,158st,159st(A-229,262,175); Trees:175,229,262,280

229 *Lecythis idatimon* Aubl.; n=4  
(Jateréu)  
FE MJP-2224fr,-2202fr,-2253st(939,83,233); Trees:83,233,962,939

497 *Lecythis lurida* (Miers) Mori; n=11  
(Matá-matá jarana)  
AN MJP-2023f1,-1980f1(39,145)
Trees:10,39,61,128,145,392,488,537,707,840,932

(LEGUMINOSAE) MIMOSOIDEA

107 Cedrelina cateniiformis (Ducke) Ducke; n = 14
   (Cedrorana, iacaiaca)
   SM MJP-2143st(364);
   Trees:10,361,364,428,445,480,972,1137,1510*
   PA MJP-2044fr,-2059fr(699,140); Trees:140,312,474,699,706

038 Dinizia excelsa Ducke; n = 31
   (Angelim vermelho)
   SM MJP-2172fr(11); Trees:11,38,1248,1476,1506,1549
   PA MJP-1718f1 &-1955fr(1016); Trees:734,890,1016,1038
   AN MJP-1907fr(591); Trees:15,32,591,633,742,837,874,883
   QU MJP-2214fr,2305fr1(228); Trees:228,295,348
   MD MJP-2222st(137); Trees:137,260
   IB MJP-1916fr(115); Trees:115,336,462,516,536,580,599,869

624 Inga acrocephala Steud.; n = 2
   SM MJP-2291fr,-1750fr(295,315); Trees:295*,315

167 Inga alba (Sw.) Willd.; n = 33
   (Ingá xixi)MJP-2351(JARI)
   SM C-135st,136st,137st(873,347,213); Trees:347,873,293
   PA MJP-2045fr,-2368st(77,1084),C-45st,46st,49st
   (85,100,174); Trees:73,77,85,100,174,611*,1084*
   AN MJP-2181st(428),C-56st(294); Trees:294,428
   QU MJP-2215st(186); Trees:181,186
   FE MJP-2257st,-2196st(567,111); Trees:111,567
   MD MJP-2121st(183);Trees:183,243,299*,339,359,375*,528,545
   IT MJP-2034fr(672); Tree:672
   IB MJP-2351st(60),C-37st,38st,39st,40st,41st,42st,203st
   (179,196,223,707,637,814,889);
   Trees:60,179,196,223,677,707,814,889

480 Inga capitata Desv.; n = 2
   MJP-2396(JARI)
   SM Trees: 295*,1584*

163 Inga edulis Mart.; n = 3
   (Ingá cipó)
   SM MJP-2144ST(543); Trees:543,313*,350*

641 Inga cf. neorensis Bentham; n = 1
   (Ingá amarelo)
   FE MJP-2255ST(249); Tree:249

642 Inga cf. panurensis Spruce ex Bentham; n = 1
   FE MJP-2256fr(326); Tree:326

388 Inga paraensis Ducke; n = 1
   (Ingá vermelho)
   IB MJP-2403fr(496); Trees:496
165 *Inga pezizifera* Benth.; *n* = 2
(Ingá grande) MJP-2396st
PA C-43st(72); Tree:72
IB MJP-2397st(833); Tree:833

166 *Inga rubiginosa* (Rich.); *n* = 19
(Ingá peludo) MJP-2669
SM MJP-2145st(413); Trees:42*,413
PA MJP-2057fr,-2129st,-2129fr,-2046fr(197,359,81,359),
Trees:81,158,160,197,358,359,448,602,963,1083*
MD MJP-2122st(203); Trees:203*,355,467,537,598
IB C-199st,201st(560,908); Trees:560,908

640 *Inga thibaudiana* DC.; *n* = 11
(Ingá cipó 2) Beck et al.-28,-10 (NY)
SM MJP-2105fr,-2167fr,-1682f1(703,137,137); Trees:137,703
PA MJP-2050fr(366); Trees:366
IB MJP-2221st,-2395f1,-2394st(813,974,919);
Trees:750,758,776*,811,825,813,919,974

644 *Inga sp.nov.*; *n* = 3
IB C-35st,194st,204st(154,715,241); Trees: 154,715,241

041 *Marmaroxylon racemosum* (Ducke) Killip; *n* = 37
(Angelim rajado)
SM MJP-2173st(1191); Trees:1191,1281,1551
PA MJP-1950f1+fr(329);
Trees:23,114,189,199,329,422,930,1025,
AN MJP-2294st(403); Trees:174,403,587,614,716,733,888,923
QU MJP-2217st(120); Trees:73,120,123,125,138,206,250
FE MJP-1853f1(668); Trees:668,994
MD MJP-1896f1(772); Trees:672,233,324*,503,756,766,772,844
IT MJP-2338st(792); Trees:792

376 *Parkia decussata* Ducke; *n* = 1
(Fava arara tucupi)
IB MJP-2352st(511); Tree:511

126 *Parkia oppositifolia* Bentham; *n* = 22
(Fava coré)
SM MJP-2146st(1268); Trees:1268*
PA MJP-2270st,-2271st(121,185); Trees:121,185
AN MJP-2371st(731); Trees:395,406,429,496,507,582,731,882,
QU MJP-2111f1(433); Trees:268,344,433,500,580,674,696,980,
FE MJP-2204st(148); Trees:148
MD MJP-2123st(453); Trees:453
IT MJP-2101f1(728); Tree:728

143 *Parkia yulei* (Harms.) Kuhlman; *n* = 14
(ESponjeira) MJP-1821 (JARI)
SM MJP-2264st(530); Tree:530
PA MJP-2131fr(569,fr.of ground); Tree:569
AN MJP-2372st(353); Trees:353*,743
QU MJP-2216st(200); Trees:200,222,880*,918*,933
MD MJP-1723f1(59); Trees: 59,326,330*,357,700
289 *Pentaclethra macroloba* (Willd.) Kuntze; n= 24  
(Pracaxi) MJP-1782  
SM MJP-2147st(366); Trees:209,366,420,454,477,489,506*,945  
PA MJP-2132st(497); Trees:40,436,470,482,497,627,840,874*  
IT MJP-2337st(403); Trees:364,375,403,478,529,538,559,624

343 *Piptadenia communis* Bentham n= 47;  
(Timbó-rana)  
SM MJP-2148st(264); Trees:78,264,812,1192,1601  
PA MJP-2047fr(710); Trees:34,214,262,675,717*,899,1023,1095  
AN MJP-2064fr,-2374afr(93,206);  
Trees:93,95,206,594,648,711,878,988,  
QU MJP-2084st,-2083st(174,150); Trees:150,174,179,279  
FE MJP-2098fr,-2197fr(713,713); Trees:420,707,713,722  
MD MJP-2124st(112); Trees:112,307,479,778,908  
IT MJP-2175fr(641); Trees:634,641,643,668,678  
IB MJP-2401st(220); Trees:220,245,400,896,905,951,841,717

616 *Zygia ampla* (Spruce ex Benth.) Pittier; n= 7  
(Jaranjeu) MJP-1432 (JARI)  
IT MJP-2339st(323); Trees:136,137,249,323,369*,475,522

**MELIACEAE**

035 *Carapa guianensis* Aubl.; n= 32  
(Andiroba)  
SM MJP-2171st(575); Trees:188,359,527,575,616,755,1158,1385  
PA MJP-2043fr(658); Trees:363,451,525,658,741,937,974,999  
IT MJP-2335st(445); Trees:372,388,445,457,467,470,573,583  
IB MJP-2390st(303); Trees:334,303,434,543,670,700,881,902

106 *Cedrela odorata* L.; n= 2  
(Cedro vermelho)  
SM MJP-1818fr(302); Tree:302  
IB MJP-2391st(878); Tree:878

489 *Guarea kunthiana* A. Juss.; n= 11  
(Jatobá vermelho)  
SM MJP-2009fr(669),C-186st,187st,188st,190st,191st,  
192st,193st(1271,1359,1196,1154,931,836,745);  
Trees:669,745,836,931,1154,1196,1271,1359  
PA C-167st,168st(947,1046); Trees:387,947,1046

724 *Guarea macrophylla* Vahl s.sp.pachycarpa(C.DC.)Penn.; n= 6  
(Jatobá vermelha 2)  
SM MJP-2011fr(1628),C-138st,139st,140st,141st  
(1409,1594,1566,1355); Trees:1355,1409,1566*,1594,1628  
IB C-200st(623); Tree:623

725 *Guarea pubescens* (Rich.) A. Juss.; n= 2  
(Jatobá peluda)  
PA C-48st(167); Tree:167  
IB C-198fr(390); Tree:390

731 *Guarea purusana* C. DC.; n= 6  
(Jatobá vermelho da várzea)  
IT MJP-2000fr(530),C-180st,181st,182st,184f1  

317
(485,525,503,443); Trees: 443, 483, 485, 503, 525, 530

726 Trichilia cf. hirta L.; n=2
(Javauba vermelha 2)
IT MJP-1937f1(977); Tree: 977
PA MJP-1813st(106); Tree: 106

569 Trichilia lecointei Ducke; n= 2
(Javauba branca) MJP-1783f1
SM MJP-2168st(1582); Trees: 470*, 1582*

727 Trichilia micrantha Bentham; n= 1
(Javauba branca 2)
SM MJP-2142st(1397); Trees: 1397

728 Trichilia quadrijuga Kunth s.sp.quadrijuga; n= 1
(Javauba branca 3)
IB MJP-2393st(871); Tree: 871

729 Trichilia schomburgkii C. DC.; n= 2
(Javauba vermelha 3)
IB MJP-2392st(1009), C-195st(965); Trees: 965, 1009

180 Trichilia septentronialis C.DC.; n= 3
(Javauba vermelha)
PA MJP-1812fr(387); Tree: 387
IT C-28st, 31st, 179st(715, 831, 983); Trees: 715, 831, 983

MYRISTICACEAE

358 Iryanthera sagotiana (Bentham) Warb.; n= 38
(Ucuubarana) MJP-1775 (JARI)
SM MJP-2012fr(1676);
Trees: 186, 1224, 1159, 62, 610, 204, 1676, 1209
PA MJP-2226st,-2272st(439, 330);
Trees: 330, 439, 588, 712, 935, 960, 1019, 1050
AN Tree: 856
FE MJP-2198st(422); Trees: 322, 422, 133, 583, 633, 747, 880, 957
MD MJP-2125st(140); Trees: 140, 613
IT C-25f1, 26f1, 206f1(891, 718, 771); Trees: 718, 771, 891
IB MJP-2356(740); Trees: 35, 192, 194, 208, 274, 492, 514, 740

354 Virola flexuosa A.C.Smith; n= 1
(Ucuuba branca)
MD MJP-2126st(894), C-161st(894); Tree: 894

356 Virola michelii Heckel; n= 50
(Ucuuba preta) MJP-1735f1
SM MJP-2149st(1042); Trees: 267, 874, 1042, 1462, 1626, 1673
PA MJP-1749f1, -1952fr(57, 368);
Trees: 1, 57, 202, 301, 310, 368, 844
AN MJP-2069st(856); Trees: 56, 74, 84, 86, 197, 761, 778, 836
QU MJP-2082st(154); Trees: 154, 227
FE MJP-2199st(473); Trees: 433, 473, 476, 483, 695, 811, 923
MD Trees: 46, 116, 383, 406, 776, 840, 953
IT MJP-2315f1(990); Trees: 733, 778, 960, 990, 994
IB MJP-2353f1(105); Trees: 105, 259, 424, 798, 832, 904, 983
PALMAE

065 *Denocarpus bacaba* Mart.; n= 17
(Bacaba) MJP-1890f1+fr
SM Tree:1684
PA: Tree:162
AN: Trees:290,635,666,698,803,951
FE: Tree:584*
MD: Trees:219,596,604,727
IT: Trees:677,738,739,854

427 *Socratea exorrhiza* (Mart.) H. Wendl.; n= 8
(Paxiúba)
MJP-1781(A-405); Trees:381,405,532*,555,619,776,1169,1680,

QUIINACEAE

638 *Quina aff. longifolia* Spruce ex Pl. & Tr.; n= 2
(Moela de mutum 2)
SM MJP-2150st(1046); Tree:1046
PA MJP-1860st(105); Trees:105

207 *Touroulia guianensis* Aubl.; n= 5
(Moela de mutum) MJP-1451
SM MJP-2151fr(1468); Trees:1468,903
MD MJP-1960f1(196),C-160st(257); Trees:196,257,618*

SIMARUBACEAE

253 *Simaba cedron* Planchon; n= 4
(Para tudo)
SM MJP-1967bf1(275); TreesA:66,275*,290,
PA MJP-2048(445) Tree:445

224 *Simaruba amara* Aublet; n= 9
(Marupá)
SM MJP-2136st(654); Trees:468*,654,975,1649
MD MJP-2127st(388); Tree:388
IT MJP-2340st(556); Trees:556,618,946
IB Tree:133

VOCHYSIACEAE

553 *Erisma laurifolium* Warm.; n= 1
(Jaboti vermelho)
PA MJP-2003f1 &-2133fr(1047); Tree:1047

722 *Erisma sp. nov.;* n= 2
(Jaboti da flor branca)
IB MJP-2028f1(273); Trees:273,448

212 *Qualea albiflora* Warm.; n= 10
(Mandioqueira lisa) MJP-1866
PA MJP-2303st(906); Trees:737,906
AN MJP-1908st(312); Trees:312,387,446,653,683,773
MD MJP-1897st(748); Trees:535,748

734 *Qualea cf. coeruacea* Aubl.; n= 6
(Mandioqueira)
FE MJP-2258st(401); Tree:401
IB MJP-2398fr(957),2354st(525); Trees:75,525,687,806,957

213 Qualea paraensis Ducke; n=39
(Mandioq. escamosa) MJP-1367f1,-1653s1;
SM MJP-2174st(821); Trees:821,1583*,1588
AN MJP-2073st(272); Trees:120,272,368,398,475,602,670,998
QU MJP-1874f1(597); Trees:30,79,92,597,612,635,729,744,760,
FE MJP-2259fr,-2260st(32,484); Trees:32,484
MD MJP-1894f1(100); Trees:95,100,214,342,393,399,823,853
IB MJP-2399st(370);
Trees:369,370,552,572,624,751*,766,783,925,

300 Vochysia obscura Warm.; n=19
(Quaruba rosa) MJP-736 (NY),1647s1
AN MJP-2374st(944); Trees:405,407,939,944,962
QU MJP-1875f1,-1990fr(398,480);
Trees:378,393,398,480,498,550,688,728
MD MJP-1901f1(115); Trees:50,115,283,473*
IB MJP-2402st(012); Trees:12,388

528 Vochysia vismiifolia Spruce ex Warm.; n=17
(Quaruba cedro da t.f.)
AN MJP-1911f1(110);
Trees:110,303,315,405,443,550*,556*,619,818
QU MJP-1876f1(670);
Trees:277,328,650,670,663,719,730,899,990

MISCELLANEOUS FAMILIES = 24 trees of 22 species

DICHAPETALACEAE

261 Tapura amazonica Poepp. & Endl. s.sp.manausensis
Prance; n=1 (Pau de bicho)
MD MJP-1628f1(282); Tree:282

EUPHORBIACEAE

336 Mabea caudata Pax & K. Hoffm.; n=1
(Taquarí)
IB MJP-2400st(716); Tree:716

527 Pera bicolor (Klotzsch) Muell.-Arg.; n=1
(Pereiro)
FE MJP-2032 &2200st(565); Tree:565

LACISTEMATACEAE

723 Lacistema aggregatum (Bergius) Rusby; n=1
PA MJP-2370f1(701); Tree:701*

Lauraceae

170 Mezilaurus lindaviana Schw. & Mez ex Glaziou; n=1
(Itaúba amarela); Beck-46(NY)
FE MJP-2201st(80); Tree:80

506 Ocotea cf. duplocolorata Vattimo-Gil; n=1
PA MJP-2360st(953); Tree:953
LEGUMINOSAE. CAESALPINIOIDEAE

189 Dialium guianense (Aubl.) Sandw.; n=1 (Jutaí pororoca)
IT MJP-2035(800); Tree:800

188 Hymenaea intermedia Ducke; n=1 (Jutaí-mirim)
FE MJP-2261st(768); Tree:768

046 Macrolobium acaciaefolium Benth.; n=1 (Arapari da várzea) MJP-2341 (JARI)
IT MJP-2341(115); Tree:115

LEGUMINOSAE. MIMOSOIDEAE

327 Styphnodendron paniculatum Poepp. & Endl.; n=1 (Tachi-rana) MJP-2301f1
MD MJP-2135st(245); Tree:245

LEGUMINOSAE. PAPILIONOIDEAE

313 Bowdichia nitida Benth.; n=1 (Sucupira amarela)
FE MJP-2203st(103); Tree:103

547 Hymenolobium sericeum Ducke; n=2 (Angelim)
FE MJP-2254st(426); Tree:426
IT MJP-2336st(652); Tree:652

MELASTOMATACEAE

344 Miconia surinamensis Gleason; n=1 (Tinteiro)
SM MJP-2152st(1687); Tree:1687

NYCTAGINACEAE

183 Neea consticta Spruce ex Schmidt; n=1 (João mole)
AN MJP-2182st(361); Tree:361

OCHNACEAE

601 Ouratea olivaeformis Engl.; n=1 (Pau de serra vermelho)
QU MJP-2218st(460); Tree:460

RUBIACEAE

061 Ferdinandusa elliptica Pohl; n=1 (Bacabinha quina)
QU MJP-2377st(388); TreeA:388

SAPINDACEAE

419 Cupania hirsuta Radlk. or C. scrobiculata Rich.n=2 (Pau de espeto)
SM MJP-2010st(1003); Tree:1003
PA MJP-1948f1(130); Tree:130

287 Toullicia acutifolia Radlk.; n=1 (Pitomba)
PA MJP-2362st(A-912); Tree:912
Sapotaceae
566 Pouteria sp.; n=1
   (Abiu amargoso)
QU MJP-2205st(381); Tree:381

008 Micropholis venulosa; n=1
   (Abiu mangabinha)
FE MJP-2262st(955); Tree:955

Tiliaceae
280 Apeiba burchellii Sprague; n=1
   (Pente de macaco); Silva-5398(JARI)
MD MJP-2128(911); Tree:911

639 Mollia lepidota Spruce ex Benth.; n=1
   Mutamba branca 2); MJP-1746
IT MJP-2343st(412); Tree:412

Unknown families: n=9
IT Tree:504(not Meliaceae)
IB MJP-2345st (56)Trees:56*,156,186,399;
   also:228,782,934(not Meliaceae)
PA Tree: 101 (not Meliaceae)

Total individuals: 1508