FRUIT AVAILABILITY AND SEED DISPERSAL IN TERRA FIRME RAIN FORESTS OF COLOMBIAN AMAZONIA

Angela Parrado-Rosselli

FRUIT AVAILABILITY AND SEED DISPERSAL IN TERRA FIRME RAIN FORESTS OF COLOMBIAN AMAZONIA

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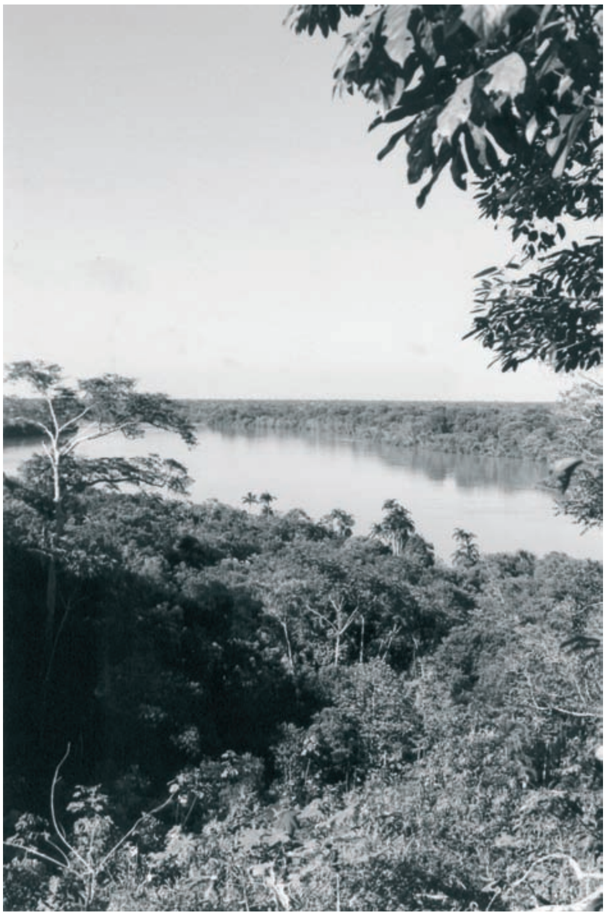

1. GENERAL INTRODUCTION

Angela Parrado Rosselli

Seed dispersal plays an important role in determining the range expansion and the spatial and genetic structure of plant populations at local and landscape scales (Levin *et al.* 2003, Nathan and Muller-Landau 2000). Seed dispersal is determined by the plant and/or disperser characteristics, the spatial pattern of reproductive adults, and their temporal variation in fruit and seed production (Nathan and Muller-Landau 2000, Levine and Murrell 2003, Schupp *et al.* 2002, Silvius and Fragoso 2003). Seed dispersal patterns vary among plant species and populations, at different distances from parents, at different habitats and at different times.

In the Middle Caquetá River region of Colombian Amazonia, several studies have been carried out in close collaboration with the Tropenbos Colombia Programme, Colombian and European Universities and local indigenous communities. Some of these studies have shown that variations in soil fertility at the high tree species rich terra firme rain forests, explain only a fraction of the observed patterns in plant distribution (Duivenvoorden 1995, Duque *et al.* 2003). Therefore, factors such as seed dispersal processes are probably affecting the population dynamics and spatial distribution patterns of trees. In this region of Colombian Amazonia, as elsewhere in the tropics, animals are the principal seed dispersal agents because most plant species have fruits adapted for animal consumption (Castaño-A. 2003). Consequently, they may be playing particularly significant roles in the regeneration ecology and spatial distribution of tree species (Janzen 1970, Nathan and Muller-Landau 2000, Schupp *et al.* 2002, Terborgh *et al.* 2002). Since animals are strongly affected by changes in fruit resource availability by selecting and feeding on what is available in time and accessible in space (Forget *et al.* 2002, Peres 1994, Van Schaik *et al.* 1993), patterns of fruit production may also affect seed dispersal processes occurring in this region of Colombian Amazonia. Furthermore, within the landscape units recognised in this region of Colombian Amazonia (Duivenvoorden and Lips 1993) the sandstone plateaus are isolated patches of open vegetation characterised by plant communities that differ substantially in composition and structure from the surrounding lowland tall forest vegetation (Arbeláez and Duivenvoorden 2004, Cleef and Arbeláez 2005, Huber 1988, Maguire 1979, Prance 1996). Therefore, these differences should be affecting their dispersal processes as well as their fruit production patterns.

This thesis presents some aspects of seed dispersal and its possible implications on the structure and diversity of tropical rain forests of Colombian Amazonia. The specific questions were 1) What are the patterns of fruit availability for animals? 2) Are some plants species, populations or communities providing fruits during periods of generalised fruit scarcity? 3) Do seed dispersal processes play explicit roles in determining composition and structure of plant communities?

In order to answer these questions, the working specific objectives, which correspond to the central chapters of the thesis were:

- To assess seasonal changes in fruit availability for animals, and to evaluate whether during fruit scarcity periods in terra firme rain forests, certain plant guilds or functional group(s) of plants would assume a dominance in the fruit availability (see Chapter 3).

- To evaluate whether seed dispersal processes of some common animal-dispersed tree species of terra firme rain forests of this region of Colombian Amazonia, with regular, predictable and synchronous fruiting patterns, are shaping the observed patterns of spatial distribution of juveniles and adults in the community (see Chapters 4, 5).
- To characterise the dispersal modes of the major vegetation types of the sandstone plateaus, as well as to describe fruiting patterns through the year (see Chapter 6).

In addition, given the vast experience in canopy research in Colombian Amazonia supported by the Tropenbos Colombia Programme, direct observations at the canopy level were an important and complementary tool for developing this thesis. Hence, methodological advances for data recording from the canopy level, particularly for documenting at fruit production are presented in Chapter 2

Finally, although this thesis aimed at obtaining a better knowledge on the ecology and the factors affecting composition and structure of Amazonian forests, this information is not necessarily relevant, useful and/or understandable for the indigenous people of the Middle Caquetá River region. Therefore, scientific research and information should be linked to the information needs of the different stakeholders (Rodríguez and Van der Hammen 2002, Van der Hammen 2003). In that way, Chapter 7 presents the process for developing a participatory approach while undertaking this research.

1.1 STUDY AREA

The study was carried out in the Middle Caquetá River region, State of Amazonas, Colombia (between 0° – 2°S and 70° – 73°W; Figure 1.1). According to Holdridge *et al.* (1971) this region is classified as Humid Tropical Forest life zone (bh-T). Mean annual temperature is 25.7 °C, and annual rainfall averages 3060 mm (Duivenvoorden and Lips 1993). Although the region does not have a marked dry season (months with less than 60 mm), rainfall decreases between December and February. The rest of the year is relatively wet with a peak in rainfall in May and June (Duivenvoorden and Lips 1993).

1.2 LANDSCAPES AND VEGETATION

Four broad landscape units have been recognised in this region: 1) the alluvial plains of Amazonian rivers, including its upland terraces; 2) the alluvial plain of the Caquetá river, including also its upland terraces (Duivenvoorden and Lips 1993); 3) the Tertiary sedimentary plain (TSP), and 4) the sandstone plateaus of Palaeozoic or Mesozoic age. Primary forests mainly dominate all landscapes with no recent evidence of disturbance. Terra firme rain forests represent around 80% of the landscapes, followed by lower proportions of inundated forests, swamps and sandstone plateaus. Our observations were restricted to the terra firme rain forests of the TSP, and to the sandstone plateaus.

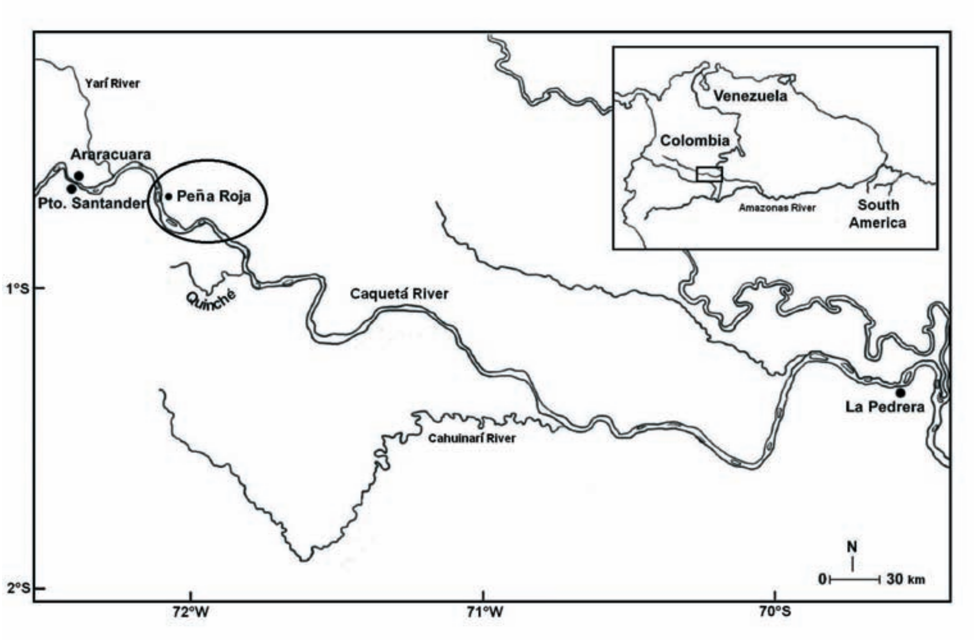

Figure 1.1. Middle Caquetá River region, State of Amazonas, Colombia. (Map from Duivernvoorden and Lips 1993)

1.2.2 Terra firme rain forests of the TSP

The TSP is the most extensive of the four broad landscape units recognised in the Middle Caquetá River region (Duivenvoorden and Lips 1993). The TSP presents a flat to undulating topography with valleys and hills of 20 to 40 m. Soils are well drained, with low mineral nutrient content, and consist of sands to clays of the Amazonian upper and lower Tertiary (Botero *et al.* 1999). Vegetation in this landscape unit is characterised by a very high species richness (Duivenvoorden and Lips 1993, Duque 2004, Londoño-Vega and Alvarez-Dávila 1997), and belongs to the most diverse forests of Northwest Amazonia (Duque 2004). The study site was located nearby the indigenous community Nonuya of Peña Roja, (0°39’05’’S, 72°04’45’’W; Figure 1.2). At this particular site, dominant plant families include Mimosaceae, Fabaceae, Lecythidaceae, Arecaceae and Dipterocarpaceae (Castaño-A 2003, Londoño-Vega and Alvarez-Dávila 1997; Appendix 1).

The forest understory is from 0 to 15 m high. Understory species include *Lepidocaryum tenue* (Arecaceae), *Attalea racemosa* (Arecaeae) and *Maieta guianensis* (Melastomataceae) (Castaño-A. 2003; see Appendix 1). The forest canopy is 25 –33 m tall, with emergents of 45 m, and 15 m as the lowest limit of the canopy (Castaño-A. 2003). The most important canopy species are *Parkia* sp. (Fabaceae), *Pseudomonotes tropenbosii* (Dipterocarpaceae) and *Monopteryx uaucu* (Fabaceae). The most common emergent species appear to be *Scleronema micranthum* (Bombacaceae) and *Eschweilera punctata* (Lecythidaceae; Castaño-A. 2003, see Appendix 1).

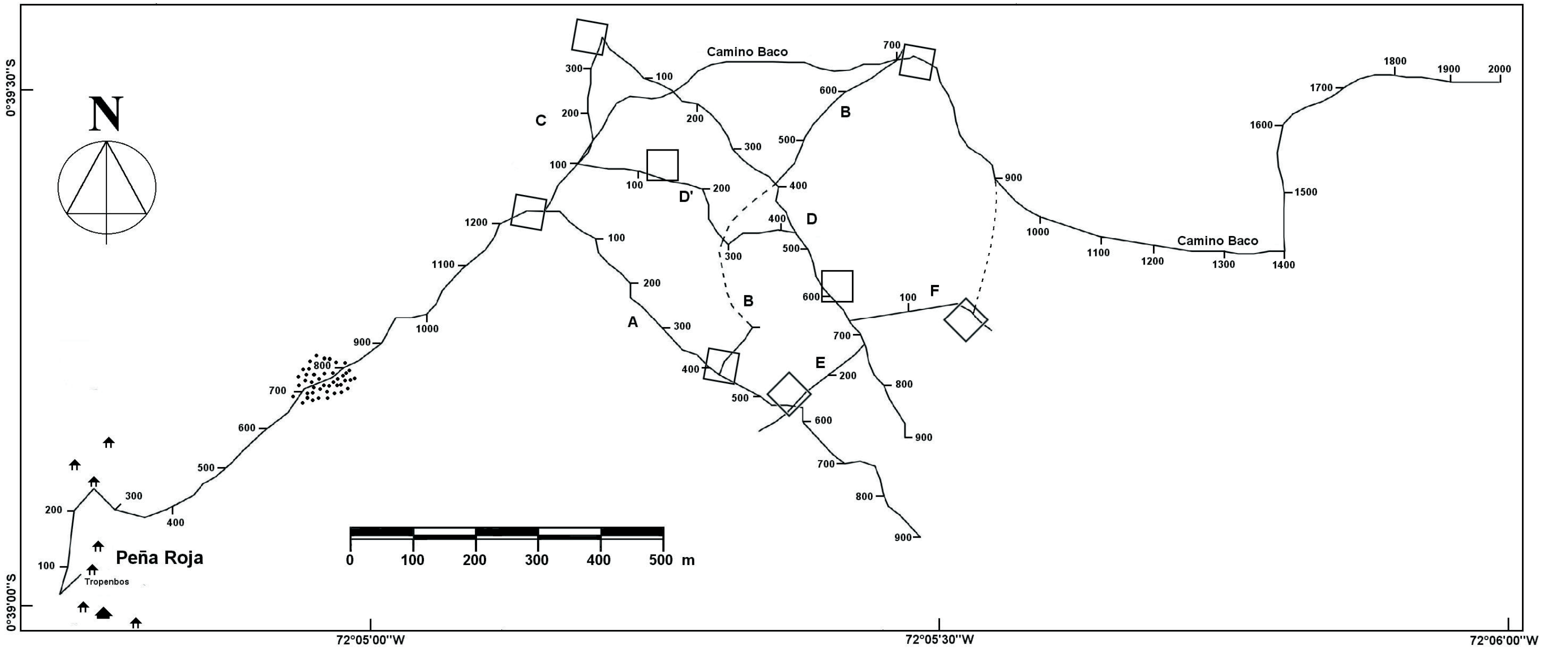

Figure 1.2. Location of the study site in the terra firme rain forest in the Tertiary sedimentary plain nearby the indigenous community Nonuya of Peña Roja.

1.2.3 Sandstone plateaus

Sandstone plateaus of the Middle Caquetá River region constitute the southernmost sandstone outcrops in the western Amazon basin. Around Araracuara, the plateau reaches altitudes of *ca*. 300–350 m a.s.l. (see Chapter 6, Figure 6.1). Northward, this plateau forms almost a continuum with the Chiribiquete sandstone massive, which rises to *ca.* 900 m a.s.l. (Estrada and Fuertes 1993). Near Araracuara the sandstones pertain to the Araracuara formation, which is of Palaeozoic age (see Chapter 6). The sandstones near Santa Isabel pertain to the Piraparaná Formation of Precambrian origin (Proradam 1979). The sandstone plateaus are characterised by extensive flattened areas, divided by deep crevices and often by the presence of sandstone blocks (Duivenvoorden and Lips 1993). They are built up of horizontally layered sandstone formations of Paleozoic or Mesozoic age, and may rise very high above the lowland landscapes. Soils are shallow nutrient-poor white sands (Cuevas 1992), waterlogged in times of rainfall, but drying out quickly during prolonged dry spells (Duivenvoorden and Lips 1993). In most cases, the plateaus form a habitat and substrate for plant communities that are quite different from that of the surrounding tall forest vegetation (Arbeláez and Duivenvoorden 2004). Plants are generally of low stature, scleromorphic, and have adapted to a permanent exposure, frequently severe water and high temperature stress, and very low soil nutrient levels (Duivenvoorden and Lips 1993). Dominant plant families include mostly herbaceous monocots such as Bromeliaceae, Cyperaceae, Eriocaulaceae, Orchidaceae, Poaceae, Rapateaceae, and Xyridaceae, as well as sclerophyllous shrubby dicotyledonous species from the families Apocynaceae, Clusiaceae, Euphorbiaceae, Melastomataceae, and Rubiaceae (Cleef and Arbeláez 2005, Duivenvoorden and Cleef 1994, Arbeláez and Callejas 1999).

1.2.4 Fauna

Although there is few information on the regional fauna, Cuadros (1993), Sarmiento (1998) and personal fieldwork data from 1996 until 2002 indicated that animal density is rather low both in hunted (selective hunting) and non-hunted sites. Ground mammals and primates comprise the greatest proportion of frugivore biomass (Sarmiento 1998, A. Parrado-Rosselli unpublished data). Agoutis (*Agouti paca*), acouchis (*Dasyprocta* spp. and *Myoprocta* spp.) seem to be the most abundant ground mammals. Spiny rats *(Proechimys* spp.) are the most abundant amongst small non-flying animals (P. Rivas unpublished data). Regarding primates, species such as *Saguinus fuscicollis, Callicebus torquatus, Saimiri sciureus, Pithecia monacus* and *Lagothrix lagothricha* seem to be the most common species in the region (Palacios and Peres 2005, Sarmiento 1998, A. Parrado-Rosselli unpublished data). Bats are very common, of which the most important species are *Carollia perspicillata, Carollia castanea, Mimon crenulatum, Glosophaga soricina* and *Tadarida brasiliensis* (P. Rivas unpublished data). There is a high diversity of the bird fauna (Cuadros 1993), which occur, in low densities. Bird-species composition between the different landscape units is quite similar except for the sandstone plateaus where few frugivorous bird species are permanent residents (Cuadros 1993, Stiles *et al.* 1995). The most important families of frugivorous birds in primary forests are Trogonidae, Pipridae, Cotingidae and Tyranidae.

1.2.5 Indigenous communities

Human occupation in the Middle Caquetá River region dates from 3000 years before present (Herrera *et al.* 1989). Nowadays, the majority of the Middle Caquetá River region is under the legal figure of *resguardo indígena* (indigenous reserve). It is inhabited mainly by indigenous communities from different ethnic groups such as Uitoto, Muinane, Andoke and Nonuya, and a minor proportion of Yukuna and Matapi. These communities have lived along the Caquetá River in small groups that do not exceed 200 inhabitants. In addition, population of settlers is low (Rodríguez 1999).

Indigenous populations have had small impact on the area's vegetation due to a low population density, and their extensive knowledge system for the management of biodiversity and resources in their territories. They have been using slash and burn methods of agriculture for centuries, properly burn and farm small plots of land, while letting soils and vegetation regenerate in plots that have recently been abandoned. On the other hand, while subsistence hunting by indigenous people is a millenary activity, hunting with commercial proposes has increased during the last years, due to the establishment of the Araracuara prison, the arrival of military forces, gold-miners and other western-people. Therefore, animal populations may have been depleted. However, there are no studies on animal densities and on the effect of hunting on animal populations.

2. COMPARISON BETWEEN TWO METHODS FOR MEASURING FRUIT PRODUCTION IN A TROPICAL RAIN FOREST[1]

Parrado-Rosselli, A., Machado, J.L., and Prieto-López, T.

ABSTRACT

We compared fruiting data derived simultaneously from fruit-traps placed on the ground and from canopy-surveyed plots in a terra firme rain forest, Colombian Amazonia. Values derived from the canopy-surveyed plots were higher than fruit-trap estimates. Fruiting patterns obtained throughout both methods were not correlated. Our results showed that the fruit-trap method does not accurately reflect fruiting patterns occurring at the highest levels of the forest, while the canopy-surveyed plots provided both quantitative and qualitative information on the canopy fruit production, and each species contribution.

RESUMEN

Comparamos los datos sobre la fructificación obtenidos simultáneamente a través de trampas de frutos dispuestas en el suelo y de parcelas monitoreadas desde el dosel de un bosque húmedo de tierra firme de la amazonia colombiana. Los valores procedentes de los monitoreos desde el dosel fueron mayores que los obtenidos con las trampas de frutos. No se encontró relación entre los patrones de fructificación obtenidos a través de los dos métodos. Nuestros resultados mostraron que el método de las trampas de frutos no refleja los patrones de fructificación que ocurren en los estratos mas altos del bosque, mientras que las parcelas en el dosel proporcionaron información tanto cuantitativa como cualitativa, y acerca de la contribución de cada especie en la producción de frutos.

Key Words: Colombian Amazonia, climbers and epiphytes, fruit mass, fruit-traps, fruiting patterns, number of fruiting species, canopy-surveyed plots.

2.1 INTRODUCTION

Seasonal timing of plant life cycle events (phenology) is linked to environmental-climatic factors, and to many biological processes including primary production, plant survival and reproduction, population biology of pollinators, seed dispersers, seed predators and herbivores. Therefore, knowledge of phenological patterns of plants is critical to understand function, structure and regeneration of forests (Chapman *et al.* 1999, Corlett and LaFrankie 1998, Foster 1982, Herrera *et al.* 1998, Schupp 1990, Smythe 1970, Van Schaik *et al.* 1993, Wright *et al.* 1999).

Within phenological processes, fruit and seed production patterns have strong effects both on plant recruitment and on many species of animals that have fruits and/or seeds as their major food source (Herrera *et al.* 1998, Van Schaik *et al.* 1993). Also, fruiting patterns may indicate the effect of inter-annual climatic

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variation in rainforests (Borchert 1998, Wright *et al.* 1999). Consequently, many studies have focused on the quantification of community-wide fruit production patterns using different methods such as fruit-traps above the forest floor, systematic surveys along transects or plots, monitoring of selected trees and observations from the canopy level (*e.g.* Borchert 1998, Chapman *et al.* 1999, Corlett and LaFrankie 1998, Di Fiore 2003, Forget *et al.* 2002, Foster 1982, Funch *et al.* 2002, Galetti and Aleixo 1998, Hemingway and Overdorff 1999, Peres 1994, Schaefer *et al.* 2002, Schupp 1990, Silvius and Fragoso 2003, Smythe 1970, Stevenson 2004, Terborgh 1983, Wright *et al.* 1999). The fruit-trap method has been widely used for assessing community-wide fruit production patterns (*e.g.* Borchert 1998, Foster 1982, Galetti and Aleixo 1998, Schupp 1990, Smythe 1970, Terborgh 1983, Wright *et al.* 1999), representing a permanent protocol for obtaining a qualitative picture of the fruiting rhythms of the forests over time. However, suitability of this method is still a matter of debate, as simultaneous comparisons between traps and other methods for recording fruit production have found contrasting results (see Chapman *et al.* 1994, Stevenson *et al.* 1998, Zhang and Wang 1995). The overall conclusion of those studies is that selection of the most suitable method will depend on the objectives proposed.

This study aimed at selecting the most suitable method for estimating canopy-community fruiting in a terra firme rain forest of Colombian Amazonia. In particular, we compared data derived simultaneously from traps placed on the ground to catch dropped fruits, and from canopy-surveyed plots, over a seven-month period. The main objective was to test which method was more informative based on the number of species and fruit mass available at the canopy level. Since lianas and climbers are important components of tropical rain forests both in species richness as well as food for frugivores (Galetti *et al.* 1994, Morellato and Leitão-Filho 1996, Nieder *et al.* 2001, Peres 1994, Schnitzer and Bongers 2002), we were particularly interested to test whether traps collected a representative sample of these growth forms.

2.2 STUDY SITE

The study was carried out from December 1999 to June 2000 in a terra firme rain forest located in the indigenous community Nonuya of Peña Roja, in the Middle Caquetá River region, Amazonas, Colombia (0°39’05’’S, 72°04’45’’W). Mean annual temperature is 25.7ºC, and rainfall averages 3059 mm per year (Duivenvoorden and Lips 1993). Although the region does not have a marked dry season (month with less than 60 mm; Duivenvoorden and Lips 1993), rainfall decreases between December and February, while the rest of the year is wet with a peak in rainfall in May and June. Dominant plant families in the study site are Mimosaceae, Fabaceae, Lecythidaceae, Arecaceae and Dipterocarpaceae (Castaño-A 2003, Londoño-Vega and Alvarez-Dávila 1997). The forest canopy is 25 to 33 m tall, with emergents of 45 m, and 15 m as the lowest limit of the canopy (Castaño-A. 2003; see Chapter 1 for detailed descriptions).

2.3 METHODS

For the canopy-surveyed plot method, four 50 x 50-m plots were established randomly with a minimum distance of 250 m between each plot, along an existing trail system throughout a 38-ha area. In each plot, between 15 and 30 m high, we constructed a central 2 x 3-m platform in a tall tree. For platform construction, we selected dense-wooded trees, with large number of branches, limited number of epiphytes, sufficient radial visibility, and without wasp and ant nests. To view the entire plot, to scan dense places not visible from the central platform, and for easily collecting plant samples, we also installed 2 to 4 observation points in the corners or sides of the plot, and hung traverse lines between tall trees. Platforms, traverse lines and observation points were reached using single rope techniques.

Each month, we recorded all plants (trees, palms, lianas, vines, hemi-epiphytes and epiphytes) bearing ripe or unripe fruits above 15 m height, within the plot boundary. Fruiting cauliflorous trees were included only if they bore fruits above 15 m height. Plants were observed with binoculars (8X 30 mm) and a telescope (20-60X 60 mm). Observed fruiting plants were mapped to the nearest 0.5 m, marked with a numbered aluminium tag (for epiphytes and climbers we marked their host trees) and monitored on subsequent visits. Since, visual counts are subjected to high inter-observer variability (Chapman *et al.* 1992), data collection was made by only one observer. It took 6 to 8 hours per month to monitor each plot (0.25 ha) depending on weather conditions.

For each plant individual, fruit mass was calculated by counting the number of fruits in three randomly selected volumes of same size of the fruit crown (modified from Chapman *et al.* 1992). Mean number of fruits of those three volumes was multiplied by the total estimated volumes of the fruit crown and by the mean dry mass of one fruit (Parrado-Rosselli *et al.* 2002). Mean dry mass of one fruit was obtained by directly collecting from the plant a minimum of 10 fruits (if available), each sampling period. Fruits were dried and weighted to nearest 0.1 g. Vouchers of each fruiting species were collected, determined up to species level when possible (otherwise to genus or family level) and deposited in the Colombian Amazonian Herbarium (COAH), and the Colombian National Herbarium (COL), both in Bogotá, Colombia.

For the fruit-trap method, thirty-six 50 x 50-cm wooden traps (collecting area 0.25 m^2), with a base of nylon cloth (mesh size 1 mm), were set 0.5 m above the ground in the same four 50 x 50-m plots selected for the canopy-surveys, for a total sampling area of 9 m^2. We placed 9 traps per plot, each one separated by at least 20 m to minimise spatial autocorrelation. Although Zhang and Wang (1995) warned about the necessity of using a large number of traps to characterise the fruiting of woody species in forests, the 0.002% of area sampled (9 m^2 in 38 ha) in our study falls within the range of 0.00003–0.017% of area sampled in other studies (see Chapman *et al.* 1994). We made surveys every 15 days to avoid decomposition, removal and damage of fruits and seeds by insects and terrestrial vertebrates. After separating between fruits, seeds, flowers, and leaves, fruits and seeds were identified to the lowest possible taxonomic level. Only fruits and seeds of canopy plant species were considered in the analysis, excluding from those of understory plants on the basis of personal observations of source plants and comparisons with herbarium specimens. Monitoring of the traps took from 4 to 6 days every 15 days (including fruit/seed identification). Fruit mass was obtained by summing dry fruit weight of all fruits found in each trap each month, and was extrapolated to a kg ha^{-1} basis.

Fruiting was measured in terms of the number of species bearing fruits each month and the amount of fruit mass per month. We discriminated between fruiting patterns of trees, and climbers and epiphytes, which include lianas, vines, parasites, hemi-epiphytes, and epiphytes. However, depending on the objectives of the project, fruiting may be differentiated, for instance, into patterns of dry and fleshy fruits, or into zoochorous, anemochorous or autochorous fruits. As we were focused on quantifying canopy-community-wide fruit production and on the selection of the most suitable method, it was unnecessary to make those distinctions.

Repeated measures analysis of variance (Zar 1984) was used to detect spatial variation in fruit abundance among plots. Variables (number of fruiting species and fruit mass) were transformed using square root transformation prior to analyses to fit the assumption of normality and for stabilising variance (Zar 1984). Differences between results derived from the two methods were obtained using product-moment correlations for that month and for one to two months prior (Chapman *et al.* 1999, Zhang and Wang 1995). All tests were performed in Statistica (V.5.5 StatSoft 1999).

2.4 RESULTS

The number of fruiting species derived from the canopy-surveyed plots was markedly higher than the one obtained through the fruit-traps. While 62 species fruiting were recorded through the canopy-plots, only 28 were recorded when using fruit-traps (Table 2.1). Mean monthly number of canopy fruiting species recorded by the canopy-surveyed plots was also higher than the one from traps (33.4 sp mo^{-1}, SD = 10.2; 8.5 sp mo^{-1}, SD = 5.3, respectively). Variation in the monthly number of fruiting species between methods was not correlated (Pearson product moment correlation r = 0.647, P = 0.165; Figure 2.1a). The number of fruiting species recorded by the canopy-surveyed plots increases from December 1999 to April 2000, and decreases during the last two months of study (Figure 2.1a). The number of fruiting species recorded by the fruit-traps showed no detectable pattern during the first four months, and decreases from April to June 2000. Both methods showed significant differences in the number of fruiting species among plots (Canopy-plots: Repeated measures ANOVA $F_{3,\ 18}$ = 4.25, P = 0.020; Fruit-traps: $F_{35,\ 210}$ = 2.17, P << 0.001). The number of fruiting species calculated for the fruit-traps showed no delay respect to number of fruiting species recorded from the canopy-plots (1 mo prior r = 0.052, P = 0.922; 2 mo prior r = 0.268, P = 0.662).

A total fruit mass of 463.1 kg ha^{-1} was derived from canopy-plots while 228.5 kg ha^{-1} were obtained from the fruit-traps (Table 2.1). Also, monthly fruit mass of the canopy-plots was higher than the fruit-traps (66.2 kg ha^{-1} per mo, SD = 35.1; 38.1 kg ha^{-1} per mo, SD = 24.0, respectively). Both methods showed that fruit mass increased during the first four months, and then decreased until the end of the study period (Figure 2.1b). However, we did not find significant correlations between patterns obtained from both methods, nor with delays of 1 or 2 months (0 mo prior r = 0.607, P = 0.202; 1 mo prior r = 0.242, P = 0.644; 2 mo prior r = 0.406, P = 0.498). We found significant differences in fruit mass between plots when using fruit-traps ($F_{35,\ 210}$ = 1.88, P = 0.004), but no significant differences when using canopy-surveyed plots ($F_{3,\ 18}$ = 0.94, P = 0.440).

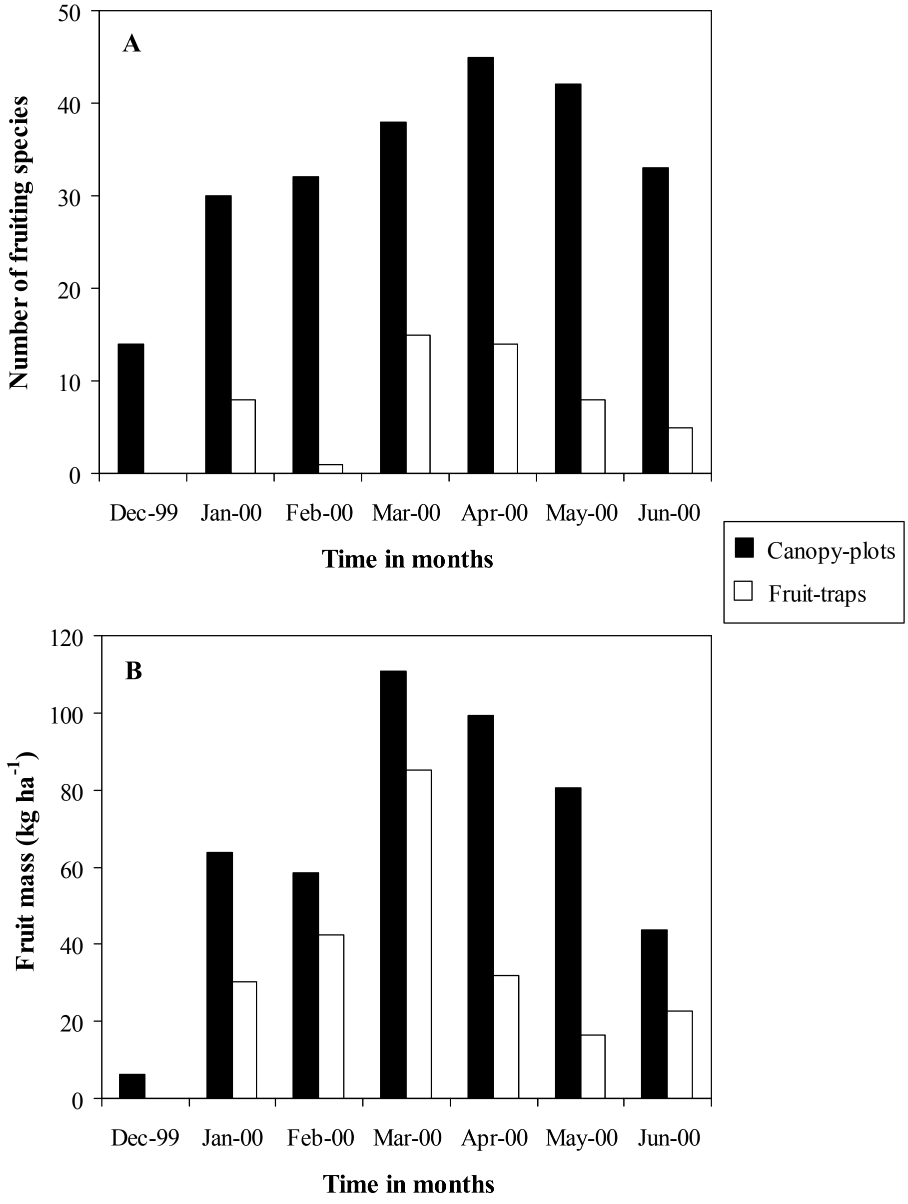


Figure 2.1. Monthly number of (a) fruiting species and (b) fruit mass (kg ha^{-1}) derived from fruit-traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest, Colombian Amazonia.

Table 2.1. Canopy-community-wide number of fruiting species and fruit mass (kg ha^{-1}) derived from fruit-traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest, Colombian Amazonia. Percentage relative to total in parentheses below.

	Sampling method					
	Canopy-surveyed plots			Fruit-traps		
	All growth forms	Trees	Climbers & epiphytes	All growth forms	Trees	Climbers & epiphytes
Total No. fruiting species	62 (100%)	43 (69.4%)	19 (36.6%)	28 (100%)	26* (92.9%)	2 (7.1%)
No. fruiting species exclusively found in one method	46 (74.2%)	29 (46.8%)	17 (27.4%)	12* (42.9%)	12* (42.9%)	0 (0%)
Total fruit mass (kg ha^{-1})	463.1 (100%)	444.6 (96.0%)	18.5 (4.0%)	228.5 (100%)	220.6 (96.5%)	7.9 (3.5%)

* (includes 8 undetermined morpho-species)

The importance of plant-guilds or functional groups differed between methods. Through the canopy-surveyed plots climbers and epiphytes corresponded to 36.6% (19 sp.) of the fruiting species and 4.0% of the total fruit mass (18.5 kg ha^{-1}), while 7.1% of the species (2 sp.) and 3.5% of the fruit mass (7.9 kg ha^{-1}) were recorded when using fruit-traps (Table 1). Families such as Clusiaceae presented the highest number of fruiting species in the canopy-surveyed plots (7 out of 8 were climbers; Table 2.2), while only one species (*Clusia* sp.) in the traps. Burseraceae, Lecythidaceae and Dipterocarpaceae were within the 5 most important plant families independently of the method, but their importance ranking changed between methods (Table 2.2). In addition, 25% of the fruits/seeds collected in the traps could not be identified up to the family level.

2.5 DISCUSSION

In our study, estimates of canopy fruit production derived from traps differed both quantitatively and qualitatively from the canopy-plots estimates. Even when considering that fruit fall can be affected by the length of fruit maturation (Foster 1982, Zhang and Wang 1995), similarities were not found neither between fruit-traps estimates obtained one or two months later than canopy-plots estimates (Zhang and Wang 1995). We found that traps do not accurately reflect the fruiting patterns occurring at the forest canopy. Consequently, the use of traps should be restricted to particular types of studies such as fruit available for terrestrial frugivores, scatter-hoarding rates, and for long-distance dispersal. In contrast, traps should be avoided in studies aimed at measuring fruit availability for arboreal and flying frugivores, because a residual quantity of fruits is sampled, as more preferred fruits do not fall into the traps in the same proportion as the ones not consumed or less preferred by frugivores (Stevenson *et al.* 1998). This will be more pronounced during fruit scarcity periods, when animals will eat a greater proportion of available fruits than when fruits are superabundant (Chapman *et al.* 1994, Terborgh 1983). Finally, fruit-traps failed to detect most of hemi-epiphytes and lianas, which are very important in the diet of fruit eating animals, particularly during lean periods (Galetti *et al.* 1994, Morellato and Leitão-Filho 1996, Peres 1994, A. Parrado-Rosselli unpublished data).

Table 2.2. List of the most important plant families based on the number of fruiting species and fruit mass (kg ha^{-1}) derived from fruit-traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest site in Colombian Amazonia.

No fruiting species				Fruit mass (kg ha^{-1})			
Canopy-surveyed plots		Fruit-traps		Canopy-surveyed plots		Fruit-traps	
Clusiaceae	8	Burseraceae	4	Burseraceae	119.2	Lecythidaceae	121.1
Lecythidaceae	7	Moraceae	4	Lecythidaceae	89.2	Euphorbiaceae	26.6
Burseraceae	6	Lecythidaceae	3	Dipterocarpaceae	82.9	Burseraceae	23.8
Chrysobalanaceae	5	Euphorbiaceae	2	Bombacaceae	77.8	Dipterocarpaceae	12.8
Euphorbiaceae	5	Undetermined	7	Fabaceae	27.0	Undetermined	16.8

Although we provide evidence that traps do not accurately capture canopy fruiting patterns, to place traps exactly where the canopy observations were performed, allowed us to demonstrate that the fruit-trap method is more sensitive to spatial variation in fruit abundance (as indicated by the significant differences in fruit mass between plots when using fruit-traps). However, the different patterns found between traps and canopy-plots might also be the result of collecting area and/or the number of traps (Chapman *et al.* 1994, Zhang and Wang 1995). In a French Guianan rainforest, Zhang and Wang (1995) found that 80 traps of 1.1 to 3.8 m^2 were not sufficient to reflect the fruiting woody species richness. In our study, the relationship between the number of traps used and the cumulative percentage of fruiting species showed that 36 traps sampled 50% of the fruiting species recorded by the two methods throughout the seven months of study, and 62% of the species recorded by the direct observations at the canopy level (Figure 2.2). Although the percent of area sampled in our study was within the range of area sampled in other studies (Chapman *et al.* 1994), a higher number of traps would have provided a better sample of the habitat-wide fruit abundance in our particular forest type.

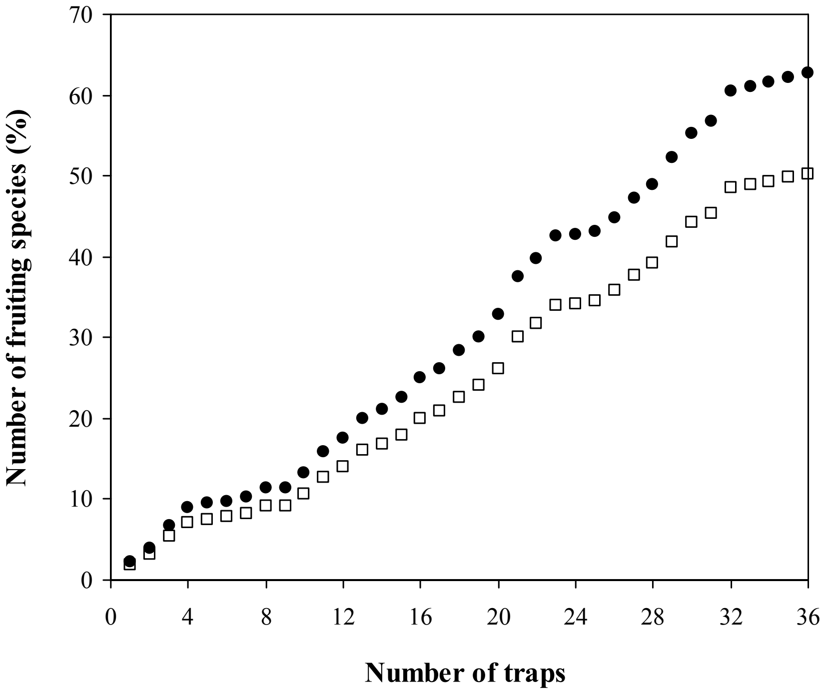
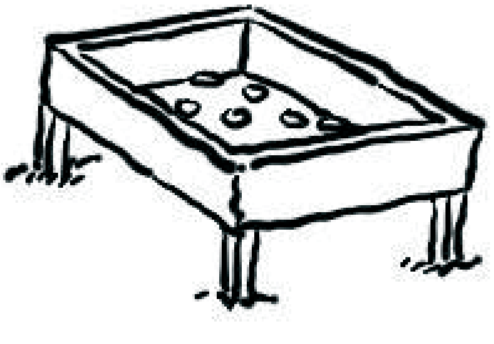


Figure 2.2. Relationship between the number of traps placed and the cumulative percentage of the number of fruiting species recorded by the canopy-surveyed plots (squares: $y = 1.4016x$, $r^2 = 0.984$), and relationship between the number of traps placed and the cumulative percentage of the number of fruiting species recorded by both methods together (dots: $y = 1.752x$, $r^2 = 0.984$).

The canopy-surveyed plots provided better estimations of habitat-wide fruiting phenology. Direct observations from the canopy level allow to quantify individual crop sizes and mass (Houle *et al.* 2004), to record availability of both unripe and ripe fruits and their variability over different fruiting periods. Also, it is possible to document fruiting of rare and scarce species hardly detected by other methods. Nevertheless, direct observations from the canopy level, have been seldom used when evaluating community-wide fruiting patterns (but see Schaefer *et al.*2002, Zhang and Wang 1995). It is generally assumed that records from the canopy are more difficult in terms of physical fitness or boldness, that they require complicated and expensive equipment, and that they can be more demanding than methods carried out from the ground. However, during the last years canopy access techniques have expanded and consolidated, and hence, it is possible to use either hi-tech' approaches such as canopy cranes or 'low-tech' methods such as single rope techniques, which are relatively inexpensive, simple, safe, portable and operable by just one or two people (Sutton 2001, Houle *et al.* 2004). Concerning logistics, we spent 1 to 1 ½ day per plot selecting the platform tree, transporting materials up to the site, setting up one platform, one traverse line, and 4 observation points, while it took only 5 hours to transport and place 9 fruit-traps in one plot. In contrast, ground-based monitoring of fruit-traps was more time-consuming than canopy-surveys, and is limited to a small proportion of habitat (Chapman *et al.* 1994). While one researcher spent 4 hours per plot for 9 traps, every 15 days, she could monitor from the canopy 0.25 ha in 5 hours, on a monthly basis (no significant change was found in 15 day periods). If a higher number of traps would have been used to sample at least 0.01% of the 38 ha area (*i.e.* 950 traps), only one researcher could not have completed the monitoring within 15 days. Finally, in order to minimise the high inter-observer variability of the canopy-surveyed plots due to the visual observations, either only one observer should make estimates, or calibrations between observers should be made to obtaining comparable estimates (Chapman *et al.* 1992).



3. CANOPY-FRUIT AVAILABILITY PATTERNS IN A TERRA FIRME RAIN FOREST OF COLOMBIAN AMAZONIA

Parrado-Rosselli, A., Castaño-A. N., Prieto-López, T., and Moreno, J.

ABSTRACT

Seasonal variations in fruit and seed abundance, affect the availability of food for frugivore species. We measured monthly changes in fruit availability for animals, at the canopy level in a terra firme rain forest of the Middle Caquetá River region, Colombian Amazonia. Fruit availability was measured as the number of individuals and species bearing fruits each month, the number of fruits and the amount of fruit mass per month. After 36 months, we recorded 166 species bearing animal-dispersed fruits at the canopy level. All estimates showed seasonal variation in canopy-fruit availability, peaking in the wettest periods of the year (April to June), while low fruiting periods occurred in the late wet and early-mid dry season (October to January). Trees and palms were the most important fruiting growth form, particularly in terms of fruit mass. Nevertheless, climbers and epiphytes provided most of the fruits during low fruiting periods of arboreal growth forms (late wet and early-mid dry season). Probably, climbers and epiphytes may be acting as an alternative fruit resource for animals, particularly during periods of fruit scarcity. Comparison with other tropical rain forests showed that fruit production in the forest studied is high in the number of fruiting species, but very poor in the monthly and total number of fruits and the amount of kilograms of fruit produced per hectare. The low fruit availability seems to explain the low vertebrate densities in this region of Colombian Amazonia.

RESUMEN

Los cambios estacionales en la abundancia de frutos afectan la disponibilidad de alimento para los animales frugívoros. Medimos los cambios mensuales en la disponibilidad de fruto para animales a nivel del dosel de un bosque de tierra firme de la región del Medio Río Caquetá en la amazonia colombiana. La fructificación se midió como el número de individuos y de especies en fruto, el número de frutos y su biomasa por mes. Durante 36 meses registramos 166 especies que ofrecieron, a nivel del dosel, frutos adaptados para la dispersión por animales. Todas las mediciones mostraron variación estacional en la disponibilidad de frutos, la cual alcanza un pico en los periodos más húmedos del año (Abril a Junio), mientras que los periodos de baja oferta ocurrieron al final de la estación lluviosa y principios de la estación seca (Octubre a Enero). Los árboles y las palmas fueron la forma de crecimiento más importante en la fructificación, principalmente en términos de la biomasa de frutos. No obstante, las trepadoras y epífitas suministraron la mayor cantidad de fruto durante los periodos de baja producción de las formas arbóreas (final de la estación lluviosa–principios de la estación seca.). Probablemente las trepadoras y epífitas pueden estar actuando como un recurso alternativo de frutos para los animales, particularmente durante los periodos de escasez. Comparaciones con otros bosques nos muestran que la producción de frutos en el bosque estudiado es alta respecto el número de especies en fruto, pero muy pobre en las cantidades mensuales y anuales de frutos y de kilogramos de fruto producidos por hectárea. La baja disponibilidad de frutos parece explicar las bajas densidades de vertebrados en esta región de la amazonia colombiana.

Key words: canopy, climbers and epiphytes, Colombian Amazonia, fruit availability, fruiting patterns, Middle Caquetá River region.

3.1 INTRODUCTION

Seed production patterns are a crucial aspect of population dynamics, forest structure and the regeneration of forests (Foster 1982, Herrera *et al.* 1998, Schupp 1990). They also have strong effects on the populations of many species of animals that have fruits and/or seeds as their major food source (Herrera *et al.* 1998, Van Schaik *et al.* 1993). Seasonal variations in fruit/seed abundance affect frugivores diets, foraging movements and their distribution within forests and habitats (Loiselle and Blake 1990, Peres 1994, Terborgh 1983, Van Schaik *et al.* 1993). Consequently, fruiting and seeding patterns determine where and how seeds are deposited, and shape the occupation patterns and spatial distribution of plant species (Levine and Murrell 2003, Schupp *et al.* 2002, Silvius and Fragoso 2003). In tropical rain forests, where 70 to 90% of plants have fruits adapted to attract fruit-eating animals (Frankie *et al.* 1974, Howe and Smallwood 1982), the study of fruiting patterns of plants may provide clues as to which animals interact with plants for the food resources they provide, and elucidate the potential demographic consequences of variation in seed production.

We assessed seasonal changes in fruit availability for animals as part of a larger study on the role of animals in the seed dispersal processes and spatial distribution of particular canopy tree species in a terra firme rain forest of Colombian Amazonia. Specifically, we focused on fruit availability at the canopy level, as understory plants are exploited by a separate set of fruit-eating animals, and are subjected to different environmental conditions than canopy plants (Loiselle and Blake 1990, Terborgh 1980, Wright and Van Schaik 1994). Fruit availability was obtained throughout canopy-surveyed plots which are known for providing accurate quantitative and qualitative information on the canopy fruit production, and each species contribution (see Chapter 2). Our main objectives were to measure monthly changes in the number of fruiting individuals and species bearing animal-dispersed fruits and seeds; the number of fruits; and the amount of fruit mass. We also evaluated whether during fruit scarcity periods certain plant guilds or functional group(s) of plants would assume a dominance in the fruit availability at the canopy level. With climbers and epiphytes as important components of the fruiting rhythms of tropical forests (Morellato and Leitão-Filho 1996), but generally underrepresented in phenological ground-surveys (Chapman *et al.* 1994; see Chapter 2), we expected to find that these growth forms would be regularly available, even during periods of low fruit abundance (Peres 1994). Finally, we discuss the possible consequences of fruit availability for animal communities of this forest site in the Colombian Amazonia.

3.2 STUDY SITE

The study was carried out from December 1999 to September 2002 in a terra firme rain forest of the Tertiary sedimentary plain (TSP) within the indigenous community Nonuya of Peña Roja, in the Middle Caquetá River region, State of Amazonas, Colombia (0°39’05’’S, 72°04’45’’W). Mean annual temperature is 25.7 °C, and annual rainfall averages 3060 mm (Duivenvoorden and Lips 1993). Although the region does not have a marked dry season (months with less than 60 mm), rainfall decreases between December and February. The rest of the year is relatively wet with a peak in rainfall in May and June. The TSP is the most extensive of the four broad landscape units recognised in the Middle Caquetá River region (Duivenvoorden and Lips 1993), covering approximately 80% of the Colombian Amazon region (Proradam 1979). The TSP presents a flat to undulating topography with valleys and hills of 20 to 40 m. Soils are well-drained, with low mineral nutrient content, and consist of sands to clays of the Amazonian upper and lower Tertiary (Botero *et al.* 1999). Vegetation in this landscape unit is characterised by a high species richness (Duivenvoorden and Lips 1993, Duque 2004, Londoño-Vega and Alvarez-Dávila 1997), and belongs to the most diverse forests of Northwest Amazonia (Duque 2004). Dominant plant families in our study site include Mimosaceae, Fabaceae, Lecythidaceae, Arecaceae and Dipterocarpaceae (Castaño-A 2003, Londoño-Vega and Alvarez-Dávila 1997). The forest canopy is 25 to 33 m tall, with emergents of 45 m, and 15 m is the lowest limit of the canopy, including plant species of the upper mid-storey, over-storey and emergent strata (Castaño-A. 2003)

3.3 METHODS

3.3.1 Data collection

Eight 50 x 50-m plots were established randomly with a minimum distance of 250 m between each plot, along an existing trail system throughout a 95 ha area. In November 1999, the number of plots initially was 4, and subsequently increased to 8 in February 2001, for a total sampling area of 2 ha. In each plot, observations were made from a central 2 x 3-m platform set up in a tall tree, traverse lines hung between tall trees, and observation points set up in the corners or sides of the plot (see Chapter 2). Heights of platforms, traverse lines and observation points ranged from 15 to 35 m, and were reached using single rope techniques.

All plants (trees, palms, lianas, vines, parasites, hemi-epiphytes and epiphytes) bearing ripe or unripe fruits above 15 m height within the plot boundary were recorded monthly (between June and September 2001 no data were collected). We included fruiting cauliflorous trees only if they bore fruits above 15 m height. Plants were observed with binoculars (8X 30 mm) and a telescope (20-60X 60 mm). They were mapped to the nearest 0.5 m, marked with a numbered aluminium tag (for epiphytes and climbers we marked their host trees) and then followed on subsequent visits. Vouchers of each fruiting species were collected, determined up to species level when possible (otherwise to genus or family level), and deposited at the Colombian Amazonian Herbarium (COAH), and the Colombian National Herbarium (COL), both in Bogotá, Colombia.

Each month we estimated the number of fruits of each plant individual by counting the number of fruits in 3 randomly selected volumes of same size in the fruit crown (modified from Chapman *et al.* 1992). Mean number of fruits of the 3 volumes was multiplied by the total estimated volumes of the fruit crown (Parrado-Rosselli *et al.* 2002). Fruit crop mass was calculated by multiplying the resulting number of fruits with the mean dry mass of one fruit. The latter was obtained by directly collecting from the plant a minimum of 10 fruits (if available), each sampling period. Fruits were dried and weighted to nearest 0.1 g. Depending on the amount of ripe fruit available per plant, we classified each plant as unripe (0-50% immature fruits relative to the total crop size) or ripe (50% ripe fruits; modified from Newstrom *et al.* 1994). We judged ripeness based on previous experience with changes in fruit colour, size, softness and appearance of dehiscence lines during maturation.

We collected data in close collaboration with indigenous field assistants. It took us 5 to 8 hours per month to monitor each plot (0.25 ha), depending on weather conditions. In an effort to decrease inter-observer variability, we conducted training trials where each observer made estimates of fruit abundance a number of times until a consistent number was obtained.

3.3.2 Data analysis

For the data analysis, we considered only canopy plant species bearing fruits and/or seeds adapted for animal dispersal. These correspond to 80.9% of the fruiting species found at this particular forest site. Animal-dispersal mode was judged based on personal observations of fruit consumption events, deduced from the morphology of the fruits and seeds of both collected and herbarium specimens, and were supplemented with information from previous studies on tropical plants and animals (*e.g.* Ascorra and Wilson 1992, Foster *et al.* 1986, Pijl 1982, Roosmalen 1985, Snow 1981, Stevenson *et al.* 2000, Wheelwright *et al.* 1984). Fruit availability was measured as the number of individuals and species bearing fruits each month, the number of fruits and the amount of fruit mass per month. As some animals may feed on unripe fruits, especially during times of fruit scarcity, as well as seed predators use to eat unripe fruits to digest the soft seeds (Blake *et al.* 1990, Foster 1977, Palacios *et al.* 1997, Snow 1971), we discriminated between patterns of ripe and unripe fruit abundance. Also, we differentiated between fruiting patterns of arboreal growth forms (*i.e.* trees and palms), and climbers and epiphytes (*i.e.* lianas, vines, parasites, hemi-epiphytes and epiphytes).

Missing data (June to September 2001) were estimated using the program TRAMO (Time Series Regression with ARIMA Noise, Missing Observations and Outliers: Gómez and Maravall 1997). Estimations can be accepted if residuals are zero-mean, uncorrelated, normally distributed, with zero skewness and kurtosis equal to 3; without residual seasonality, nor non-linearity, and their signs randomly distributed (Appendix 2). Repeated measures analysis of variance (Zar 1984) was used to detect spatial variation in fruit abundance among plots. Variables (number of fruiting individuals, species, fruits and fruit mass) were transformed using square root transformation prior to analyses to fit the assumption of normality and to stabilise the variance (Zar 1984).

Duration and frequency of fruiting was determined only for the species with more than 5 fruiting individuals monitored (as suggested by Frankie *et al.* 1974). Three duration classes were used: brief fruiting (< 1 mo), intermediate fruiting (1 to 5 mo), and extended fruiting (> 5 mo; Chapman *et al.* 1999, Newstrom *et al.* 1994). Frequency classes were sub-annual (regular patterns < 12 mo), annual (regular 12 mo pattern), supra-annual (regular pattern > 12 mo), or continuous (some individuals always fruiting). Plants with no duration and/or frequency pattern detectable in our data set were considered as irregular.

3.4 RESULTS

From December 1999 to September 2002 we recorded a total of 387 individuals in 166 species and 43 families bearing animal-dispersed fruits at the canopy level (Table 3.1; Appendix 3). Twenty-seven morpho-species could not be identified to species level. Mean monthly number of individuals ha^{-1} and species ha^{-1} fruiting was 28.8 and 20.4, respectively (Table 3.2). Each month, there was an average of 12638 fruits ha^{-1} and 24.4 kg ha^{-1} of fruit mass. Ripe fruit availability was markedly lower, averaging 9.7 individuals ha^{-1} mo^{-1}, 8.1 species ha^{-1} mo^{-1}, 2145 fruits ha^{-1} mo^{-1} and 4.6 kg ha^{-1} mo^{-1}. In general, fruit availability increased with rainfall, a peak was reached (March-April), and then decreased until the late wet and early dry season (Figure 3.1). Peaks and troughs were more pronounced in terms of the number of fruits and fruit mass. All estimates showed that fruit availability was lower and less seasonal in 2001 than in 2000 and 2002. Patterns of ripe fruit availability were similar to the canopy-community-wide patterns in terms of the number of individuals, species, and even, fruit mass, while the number of ripe fruits did not show seasonal changes and was constantly low through the time (Figure 3.1). The number of fruiting individuals, species and fruits was not statistically different among plots (No. individuals Repeated-measures ANOVA $F_{3,\ 87} = 1.63$, $P = 0.187$; No species $F_{3,\ 87} = 1.12$, $P = 0.346$; No. fruits $F_{3,\ 87} = 1.02$, $P = 0.390$). However, fruit mass differed significantly between plots located in hills, and plots in valleys ($F_{3,\ 87} = 6.42$, $P = 0.001$; Wilks's lambda = 0.572, Rao's R = 10.459; df = 2, 28; $P << 0.001$).

Table 3.1. Total number of fruiting individuals, species, families, number of fruits and fruit mass obtained from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. Percentages relative to the total in parentheses below.

Growth form	No. fruiting individuals	No. fruiting species	No. fruiting families	No. fruits	Fruit mass (kg)
Arboreal (trees and palms)	227	107	25	308125	1050.2
	(58.7%)	(64.5%)	(58.1%)	(57.8%)	(89.2%)
Climbers	149	57	16	224961	127.5
(lianas, vines, hemi-epiphytes and parasites)	(38.5%)	(34.3%)	(37.2%)	(42.2%)	(10.8%)
Epiphytes	11	2	2	248	0.01
	(2.8%)	(1.2%)	(4.7%)	(<< 0.1%)	(<< 0.01%)
Total	387	166	43	533334	1177.6

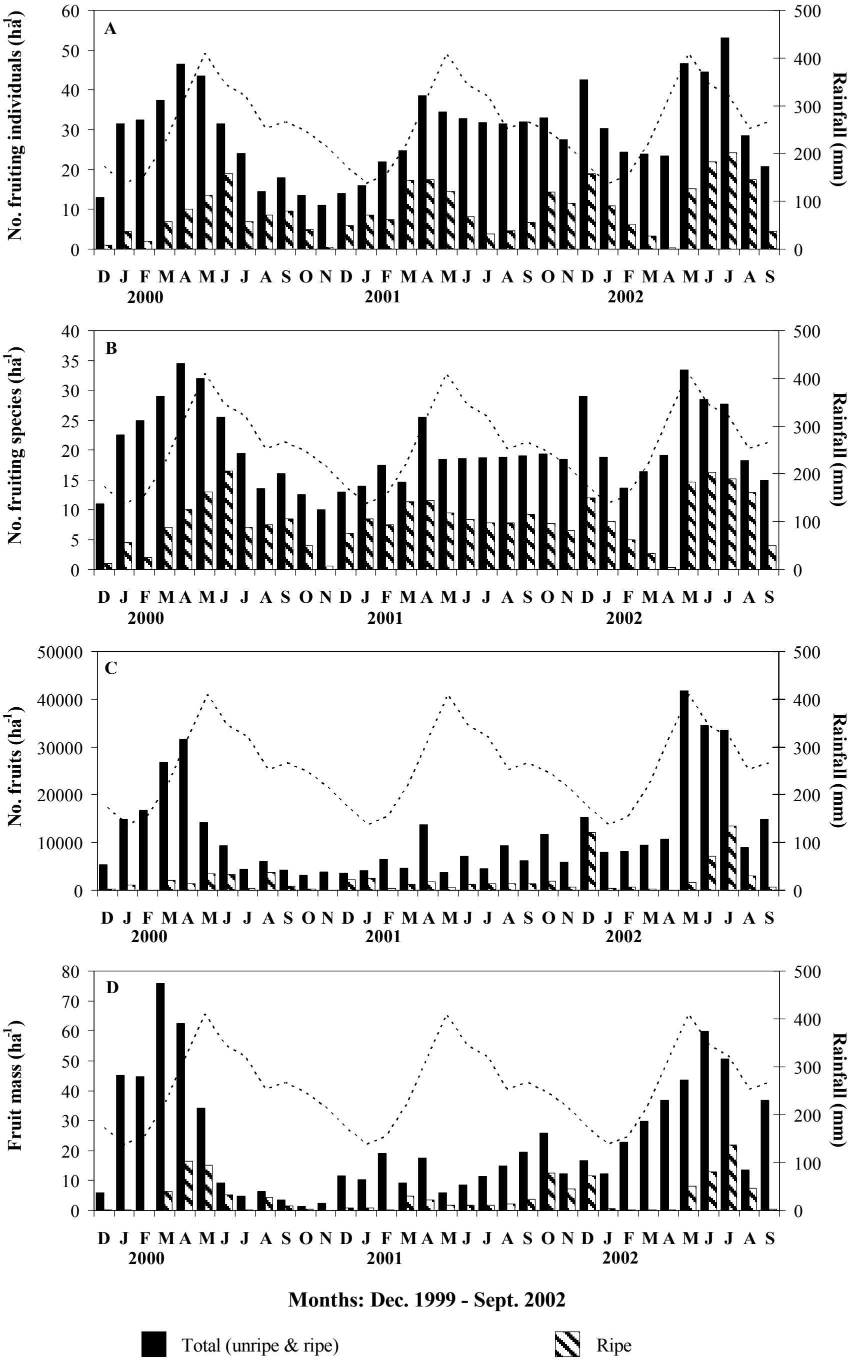


Figure 3.1. Canopy-community-wide fruiting patterns obtained from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. Missing data from June to September 2001 estimated using the program TRAMO (Gómez and Maravall 1997). Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.

Table 3.2. Mean monthly number of fruiting individuals, species, fruits and fruit mass ha^{-1}, and standard deviation (SD) recorded from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia.

	All growth forms				Trees and palms		Climbers & epiphytes	
	Total		Ripe					
Fruit production measure	Average (ha^{-1} mo^{-1})	SD	Average (ha^{-1} mo^{-1})	SD	Average (ha^{-1} mo^{-1})	SD	Average (ha^{-1} mo^{-1})	SD
No. fruiting individuals	28.8	11.5	9.7	6.4	17.4	9.0	11.4	7.0
No. fruiting species	20.4	7.0	8.1	4.3	12.5	6.0	7.8	3.5
No. fruits	12638	10544	2145	3047	7330	6297	5328	6493
Fruit mass (kg)	24.4	20.3	4.6	5.7	21.3	19.1	3.1	4.0

3.4.1 Fruit availability per growth forms

Trees and palms were the most important growth form fruiting in this forest site, particularly in terms of fruit mass (Table 3.1). There was a monthly average of 17.4 individuals ha^{-1} and 12.5 species ha^{-1} of trees and palms fruiting, providing 7330 fruits ha^{-1} mo^{-1} and 21.3 kg ha^{-1} mo^{-1} of fruit mass (Table 3.2). Mean monthly number of individuals and species of climbers and epiphytes fruiting was 11.4 ha^{-1} and 7.8 ha^{-1}, respectively. They produced 5328 fruits and 3.1 kg ha^{-1} mo^{-1} of fruit mass. Fruiting of trees and palms increased with rainfall during 2000, decreased from the middle of the wet season, and then increased again after the mid wet season of 2001 (Figure 3.2). During the dry season of 2001, all estimates showed high fruiting of trees and palms. The fruiting pattern of climbers and epiphytes was less seasonal and did not exhibit peaks as high as trees and palms (Figure 3.2). Climbers and epiphytes peaked after the middle of the wet season when the fruiting of trees and palms was very low. This trend was particularly marked in 2000 and 2002 regarding the number of fruiting individuals, species and fruits, but weaker in terms of fruit mass (Figure 3.2).

3.4.2 Floristic composition of fruit availability

The importance of plant families, in the canopy-community fruiting patterns, differed between estimates (Table 3.3). The most important family regarding the number of fruiting individuals and species was Clusiaceae, consisting mainly of climbers. The liana family Marcgraviaceae and the tree family Lecythidaceae produced the greatest number of fruits and fruit mass, respectively (Table 3.3). At the species level, the lianas *Satyria panurensis* (Ericaceae) and *Souroubea guianensis* (Marcgraviaceae) presented the highest number of fruiting individuals and fruits, respectively (Table 3.4). In contrast, the five species providing the highest fruit mass were all trees, of which *Scleronema micranthum* (Bombacaceae) exhibited the highest values (Table 3.4).

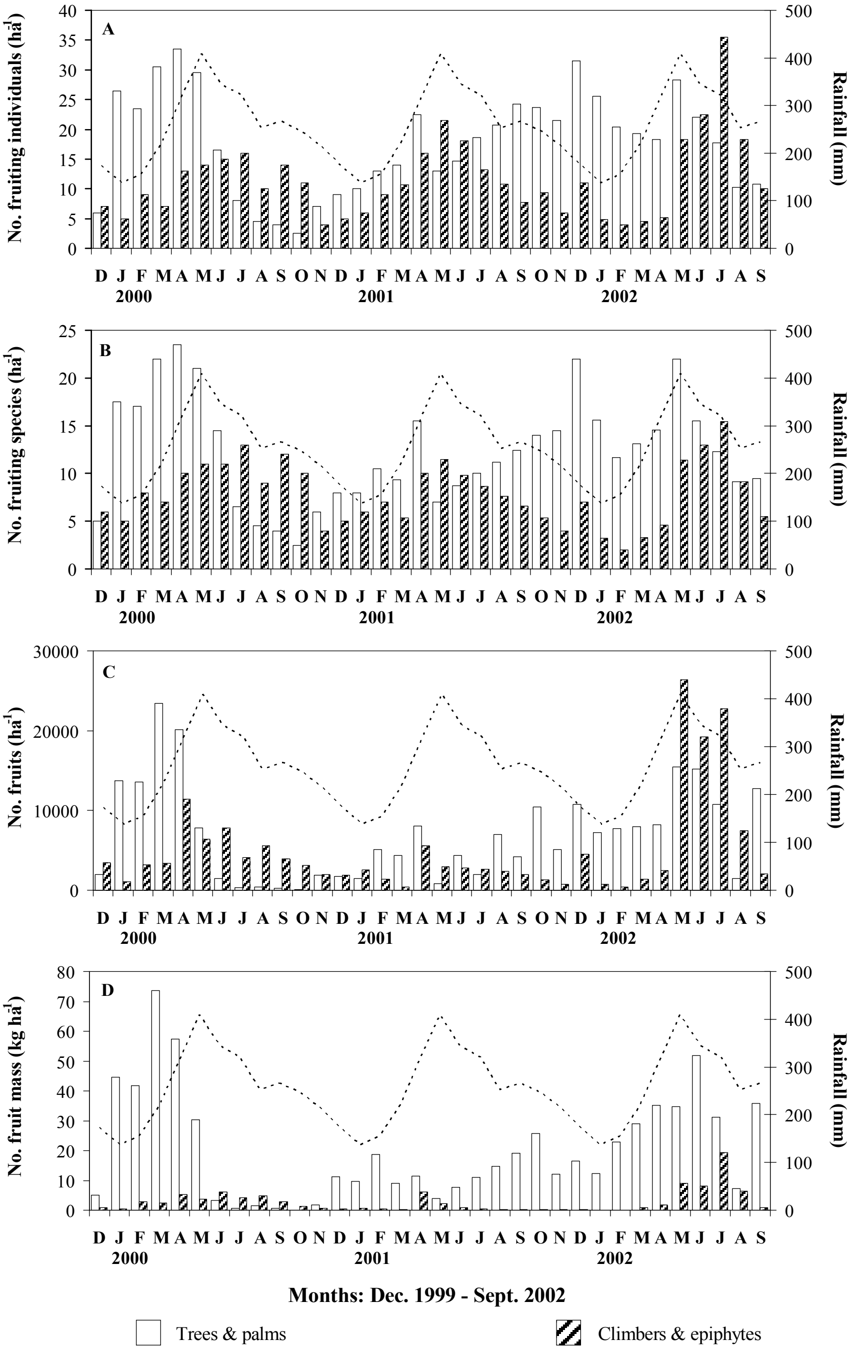


Figure 3.2. Fruiting patterns of trees and palms, and climbers and epiphytes obtained from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. Missing data from June to September 2001 estimated using the program TRAMO (Gómez and Maravall 1997). Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.

Table 3.3. List of the most important fruiting plant families from recorded from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia.

Family	No ind.	Family	No species	Family	No fruits	Family	Fruit mass (kg)
Clusiaceae	48	Clusiaceae	17	Marcgraviaceae	86639	Lecythidaceae	247.48
Lecythidaceae	28	Lecythidaceae	10	Burseraceae	73017	Bombacaceae	216.88
Convolvulaceae	26	Euphorbiaceae	9	Lauraceae	50496	Burseraceae	147.92
Marcgraviaceae	25	Myristicaceae	9	Lecythidaceae	43631	Mimosaceae	81.51
Sapotaceae	22	Sapotaceae	9	Clusiaceae	37965	Chrysobalanaceae	65.49

We recorded 21 species with more than five individuals bearing fruit. Nine out this 21 species presented extended fruiting patterns (> 5 mo duration), five intermediate patterns (1 to 5 mo), while none fruited briefly (< 1 mo; Table 3.5). Seven species could not be classified into any of the three duration classes, so they were considered as irregular. Based on the fruiting frequency, 18 out of these 21 species showed a marked seasonality (Table 3.5). Eleven species fruited supra-annually, six annually, and only one fruited on a sub-annual basis. No frequency pattern was detectable for three species (Table 3.5). Figures 3.3 and 3.4 show fruiting patterns of the five most important species of climbers and trees, respectively.

Table 3.4. List of the most important fruiting plant species per growth from recorded from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. T = tree, L= liana, Ep = Epiphyte.

Species	Growth form	No ind.	Species	Growth form	No fruits	Species	Growth form	Fruit mass (kg)
Satyria panurensis	L	18	*Souroubea guianensis*	L	75793	*Scleronema micranthum*	T	216.9
Souroubea guianensis	L	14	*Eschweilera punctata*	T	35702	*Eschweilera punctata*	T	145.0
Chrysophyllum sanguinolentum	T	9	*Buchenavia tetraphylla*	T	32935	*Protium altsonii*	T	78.6
Licania apetala	T	8	*Licaria* cf. *guianensis*	T	32696	*Parkia panurensis*	T	67.1
Codonanthe crassifolia	Ep	8	*Curarea* sp.	L	23494	*Protium polybotryum*	T	50.3
Vantanea spichigeri	T	8						
Eschweilera coriacea	T	8						

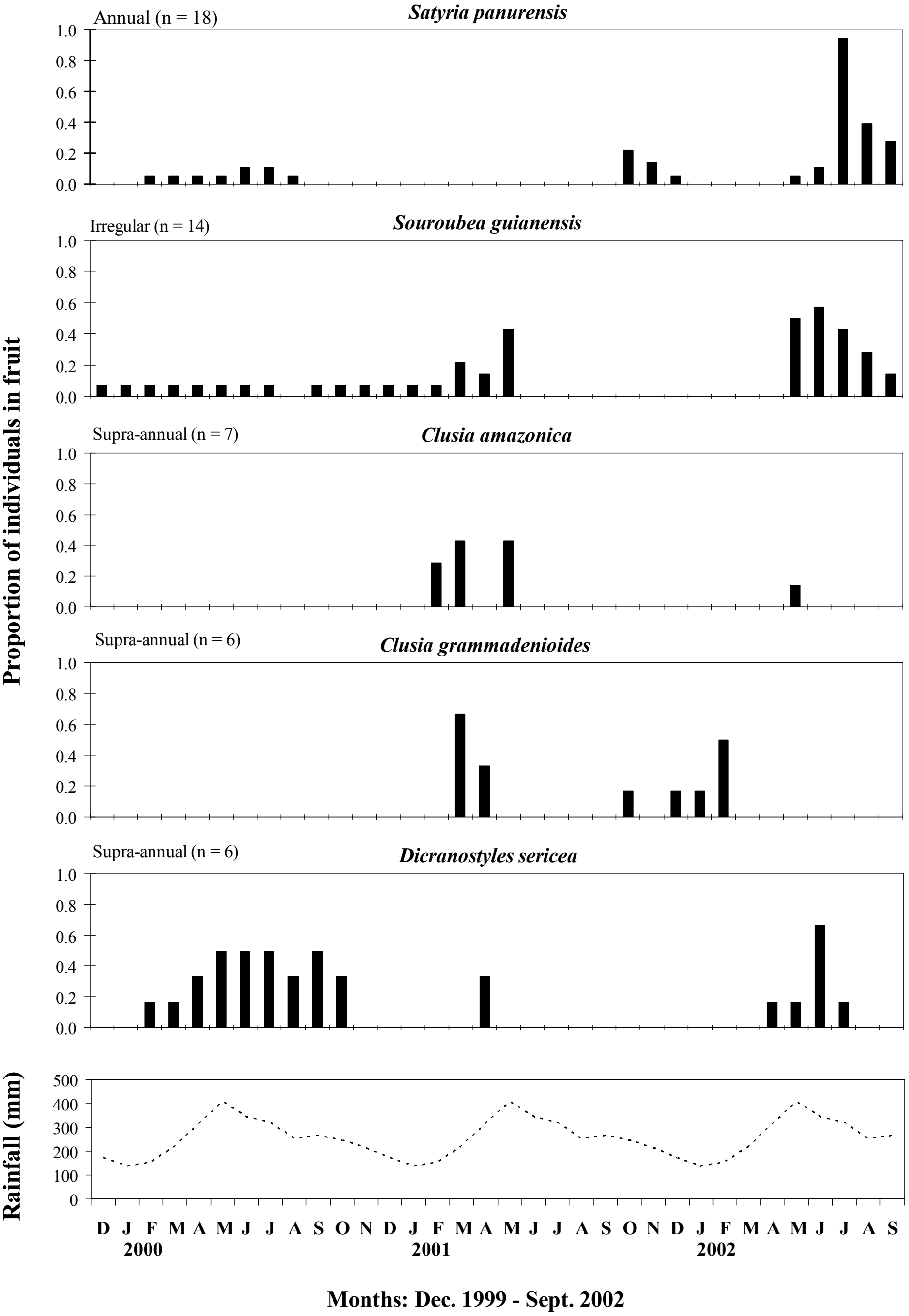


Figure 3.3. Fruiting patterns of the five species of climbers with the highest number of fruiting individuals monitored from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.

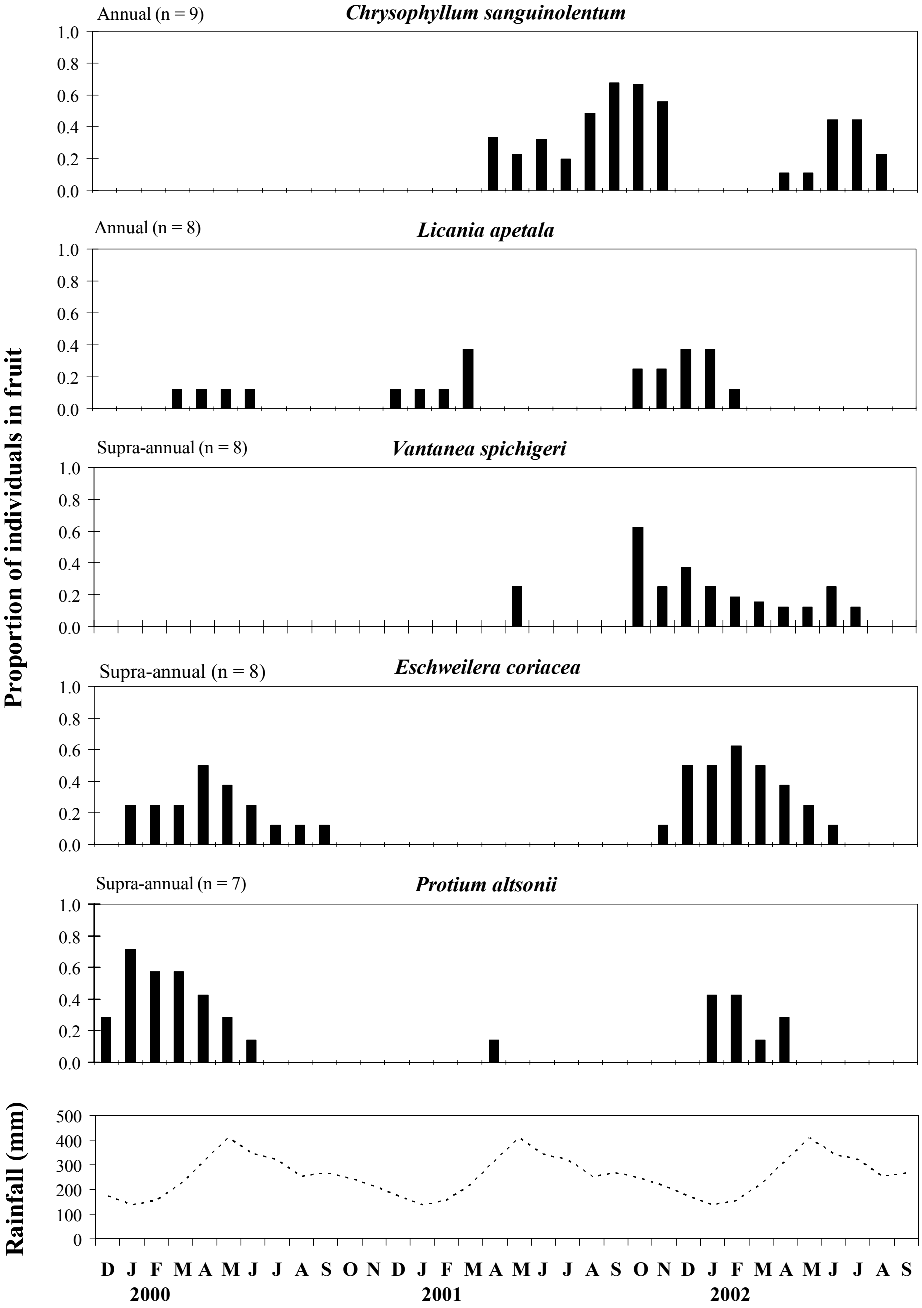


Figure 3.4. Fruiting patterns of the five tree species with the highest number of fruiting individuals monitored from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.

Table 3.5. Plant species with more than 5 fruiting individuals, duration and frequency patterns obtained from December 1999 to September 2002 at the canopy level in a terra firme rain forest, Colombian Amazonia. T = tree, L= liana, Ep = Epiphyte.

Plant species	Growth form	No. individuals	Duration pattern	Frequency pattern
Satyria panurensis	L	18	Extended	Annual
Souroubea guianensis	L	14	Irregular	Irregular
Chrysophyllum sanguinolentum	T	9	Extended	Annual
Codonanthe crassifolia	Ep	8	Intermediate	Supra-annual
Licania apetala	T	8	Intermediate	Annual
Vantanea spichigeri	T	8	Extended	Supra-annual
Eschweilera coriacea	T	8	Extended	Supra-annual
Clusia amazonica	L	7	Irregular	Supra-annual
Eschweilera punctata	T	7	Extended	Supra-annual
Protium altsonii	T	7	Extended	Supra-annual
Clusia grammadenioides	L	6	Irregular	Supra-annual
Dicranostyles sericea	L	6	Irregular	Supra-annual
Pouteria guianensis	T	6	Extended	Annual
Scleronema micranthum	T	6	Intermediate	Annual
Buchenavia tetraphylla	T	5	Extended	Annual
Clusia gaudichaudii	L	5	Irregular	Irregular
Clusia spathulifolia	L	5	Irregular	Irregular
Dacryodes chimantensis	T	5	Extended	Supra-annual
Endlicheria cf. *dysodantha*	T	5	Irregular	Supra-annual
Maripa cf. *reticulata*	L	5	Intermediate	Supra-annual
Micrandra spruceana	T	5	Intermediate	Sub-annual

3.5 DISCUSSION

Similarly to most tropical communities, fruiting in this terra firme rain forest of Colombian Amazonia displays seasonal variation, peaking in the wettest periods of the year (April to June), while low fruiting periods tend to occur in the late wet and early-mid dry season (October to January; *e.g.* Forget *et al.* 2002, Palacios and Rodríguez 2001, Peres 1994, Silvius 2002, Stevenson 2004, Stevenson *et al.* 2000). Ripe fruit availability in terms of the number of fruiting individuals, species and fruit mass also increased with rain. However, this pattern did not hold when considering the number of fruits. Plants may be ripening their fruits over a long time in order to enhance seed dispersal and to reduce competence for seed dispersers (Foster 1982, Smythe 1970).

There were important differences in the fruiting patterns between years: while 2001 was a low production year; 2000 and 2002 were both high production years (Figure 3.1). Although these differences can be due to the TRAMO missing data estimations (June to September 2001), residuals showed that estimated data appear to fit the patterns of available information; thus we assumed that differences between years are due to biological factors. On the one hand, it is well known that even in relatively aseasonal habitats, seasonal variation in weather plays an important role in shaping the phenology of many plants (Borchert 1998, Corlett and LaFrankie 1998, Van Schaik *et al.* 1993, Wright and Van Schaik 1994). This variation creates a strong tendency for high fruit production years to alternate with low fruit production years (Wright *et al.* 1999). In our study site, during the low fruit production year 2001, Téllez (2003) reported slightly over 3500 mm of rain, which was higher than the multi-annual records (1979-1990) of the area (3060 mm; Duivenvoorden and Lips 1993). She also found that December 2001 and January 2002, which are the typical dry months, rainfall was as high as in the wettest months (December 2001 = 320 mm, January 2002 = 260 mm), explaining the high numbers of fruiting individuals, species and fruits found in those months. On the other hand, despite the general community-level synchronisation, most species and individuals were recorded once, suggesting that they are not reproducing annually, as occurs in other tropical forests where only a small proportion of the adult tree species and individuals reproduce in a given year (Chapman *et al.* 1999, Corlett and LaFrankie 1998, Foster 1982, Van Schaik *et al.* 1993). Moreover, half of the most important species fruiting in our forest site presented supra-annual patterns of fruit production. Variability and intensity of such annual and multi-annual trends, and factors governing them may be recorded through longer-term monitoring.

3.5.1 Fruiting at the species level and plant-group level

Although climbers and epiphytes are important components of tropical rain forests both in species richness as well as food for frugivores (Duque 2004, Galetti and Pedroni 1994, Morellato and Leitão-Filho 1996, Nieder *et al.* 2001, Peres 1994), their actual role in fruit availability is not well known, as these growth forms tend to be under-represented in phenological studies carried out from the ground (Chapman *et al.* 1994; see Chapter 2). During our 34 mo systematic canopy-surveyed plots, we found that: 1) climbers and epiphytes provided a considerable amount of fruits; 2) they exhibited high number of fruiting individuals and species, 3) the families and species with the highest number of fruiting individuals and fruits were made up of lianas, and 4) they fruited throughout the year, and provided most of the fruits during low fruiting periods of arboreal growth forms. As this pattern seems to be year to year consistent, many tropical fruit-eating animals could depend on it, and hence, climbers and epiphytes may be acting as an alternative fruit resource for animals, particularly during fruiting troughs. Our results coincide with other studies, where fruiting patterns of climbers were shown to be out of phase or less seasonal than trees (Morellato and Leitão-Filho 1996, Peres 1994). However, fruit mass produced by these growth forms is very low, and will not be available in the forest floor in the same proportion as the fruit mass produced by trees and palms, and will not meet the energetic requirements of animals such as tapirs and peccaries, which are highly dependent on fruit fall. For example, 8 g climber fruits represents a much greater fraction of the daily nutritional requirements of a 200 g spiny-rat than a 30 kg peccary. Thus, we believe that during lean periods, small and mid-bodied arboreal and terrestrial animals take more advantage of fruits of climbers and epiphytes than large-bodied mammals. The later will probably respond to the low fruiting periods by moving over greater ranges, or switching to other habitats (Fragoso *et al.* 1998). Research on the nutritional value of fruits, and on dietary habits of fruit eating animals, will provide more evidence on the importance of these growth forms for the frugivore community of this and other Amazonian forest sites.

3.5.2 Considerations on the fruit availability

In the same way that high species-rich forests result in very low densities of the individual species, community-wide fruiting patterns of our forest site may be exhibiting similar trends. Thus, the high species richness of the TSP forests, which is comparable to the most diverse forests of NW Amazonia (Castaño-A. 2003, Duivenvoorden and Lips 1993, Duque 2004), also will result in a high number of species with few individuals providing fruits. On the other hand, fruit availability in this forest site was found to be extremely poor in the monthly and total number of fruits and the amount of kilograms of fruit produced per ha. For instance, in a 1.5 ha terra firme rain forest along the Surumoni River in Venezuela Schaefer *et al.* (2002), who sampled a small set of fleshy-fruited species, found that the greatest number of fruits produced in one month above 16 m height was approximately 300,000 fruits ha^{-1}, while in our study, the highest monthly number of fruits ha^{-1} was 41,777 (May 2002). In an other study, Stevenson (2004) found that in a tropical rain forest on the eastern border of Tinigua National Park in Colombia, the 21 most important plant species producing ripe fleshy fruit between February 2000 and January 2001 (12 mo) produced 658.9 kg ha^{-1}, while the 166 species recorded in our study site produced 785.4 kg ha^{-1}, during 34 mo (277.2 kg ha^{-1} y^{-1}). Although Stevenson sampled trees with a diameter at breast height (dbh) of $\geq$ 10 cm, we believe that the $\geq$ 15 m height used in our study is an equivalent criterium for sampling adult-reproductive individuals. In addition, data available on fruit mass from other sites in Peru, Panama and Puerto Rico, showed higher values than our study (Foster 1982, Gentry 1990, Lugo and Frangi 1993, Terborgh 1983). However, they are not strictly comparable as these values are given in annual wet fruit weight.

As forests growing on poor soils are generally less productive than those growing in fertile soils (Defler 1996, Terborgh and Van Schaik 1987), the small crops and the low fruit mass recorded in our study site can be a consequence of the TSP soils, which are poorer in minerals, nutrients and N than its equivalents in Peru and Ecuador (Lips and Duivenvoorden 2001). Our results also agree with Peres (1994) findings in a terra firme forest in the upper Urucu River, Brazilian Amazonia, where the low fruit abundance was a consequence of its very poor quality of soils. In addition, he found that várzea forests sustained by nutrient rich soils tended to have greater wildlife biomass than those in nutrient-poor terra firme forests (Peres 1994). Thus, the low fruit abundance recorded in the Urucu terra firme forest largely explained why many frugivorous bird and primate species were surprisingly rare, even though their numbers had been never depressed by selective hunting (Peres 1994). Although in our study area there is few information on the local fauna, Cuadros (1993), Sarmiento (1998) and personal fieldwork data from 1996 until 2002 indicated that animal density is rather low both in hunted (selective hunting) and non-hunted sites. Additionally, in the adjacent Lower Apaporis River, in Colombian Amazonia, aggregate biomass densities of diurnal primates are amongst the lowest recorded for any non-hunted forest in western Amazonia and else where in the tropics (Palacios and Peres 2004). Moreover, their home ranges and mean length of daily ranges are larger than those recorded in other sites (Defler 1996, Palacios and Rodríguez 2001). Therefore, in agreement with Peres (1994) the small crops, the low fruit mass, the low availability of ripe fruits throughout the year in our forest site, and the great extension of the TSP all over the Colombian Amazon region (Proradam 1979) appear to explain the low frugivore densities, as they are forced to forage over large ranges in order to search for food and to shift or to restrict to other habitats, particularly during certain year periods (Altrichter *et al.* 2002, Palacios and Rodríguez 2001, Palacios *et al.* 1997, Peres 1994, Stevenson *et al.* 2000, Terborgh 1983). Such effects of low fruit availability are expected to be significant not only for arboreal animals but also for terrestrial animals, since many of them are highly frugivorous and dependent on fruit fall (Bodmer 1991, Forget *et al.* 2002, Gayot *et al.* 2004).

Impacts of low fruit availability on the populations of several species of animals that have seeds as their major food will also influence seed dispersal processes (including predation) of each particular species (Forget *et al.* 2002, Herrera *et al.* 1998, Schupp 1990, Silvius and Fragoso 2003). Thus, some species producing few fruits during the fruiting peaks of the forest, may be dispersal limited, because dispersers would prefer species with larger crops (Rozo-Mora and Parrado-Rosselli 2004; see Chapter 4). In contrast, for other species, fruiting synchronously may enhance each others dispersal by stimulating seed-predator satiation, and by attracting more dispersers than each would alone (Foster 1982, Van Schaik *et al.* 1993, Wheelwright 1985). For others, offering few ripe fruits over a long time or during scarcity periods (*e.g.* climbers) can be a strategy for avoiding competition for seed dispersers (Foster 1982, Smythe 1970). Studies on vertebrate and frugivore density in this area of the Amazon, and comparisons with the soil-nutrient rich and higher fruit productive várzea forests will provide an increased understanding of the impacts of seasonal rhythms of fruit supply in animal communities. A comprehensive approximation of plant life-history and evolution, and population dynamics of animal and plant communities, and therefore a robust basis for developing management options will be obtained only through increased knowledge of patterns of supra-annual variation in seed production.

4. DIURNAL PRIMARY SEED DISPERSAL OF *Dacryodes chimantensis* AND *Protium paniculatum* (BURSERACEAE) IN A TERRA FIRME RAIN FOREST OF COLOMBIAN AMAZONIA[1]

Rozo-Mora, M.C., and Parrado-Rosselli, A.

ABSTRACT

Diurnal primary seed dispersal of *Dacryodes chimantensis* and *Protium paniculatum* (Burseraceae) was studied in a terra firme rain forest of Colombian Amazonia. From December 1999 to June 2000 we recorded frugivore visits, fruit removal and primary seed dispersal in 5 individuals per species. We found that mean tree height, area of canopy projection, diameter at breast height (dbh), and fruit crop sizes of *D. chimantensis* were larger than in *P. paniculatum.* During the fruiting season of *D. chimantensis,* mean percentage of ripe fruits relative to the fruit crop size ranged between 3 and 21%, while percentage of ripe fruits of *P. paniculatum* ranged between 1 and 15%. Diurnal frugivore activity was observed in 4 out of the 5 individuals of *D. chimantensis,* while no diurnal frugivory was observed in the *P. paniculatum* individuals. Only the parrots, *Amazona festiva* and *A. amazonica*, fed on *D. chimantensis* fruits. They removed an average of 1.8% fruits per tree, but they did not carry away viable seeds from the parent tree (primary seed dispersal). In the traps located under the area of canopy projection, the number of intact fruits, picked and damaged by animals was similar for both species. The small fruit crop sizes, the low number of ripe fruits and the low rate of fruit crop reduction, together with the low number of visits, fruit removal and diurnal primary seed dispersal by frugivores suggest that these two species are dispersal limited. The impact of the low seed dispersal by animals on the spatial distribution patterns of these tree species is discussed.

RESUMEN

Se estudió la dispersión primaria diurna de las semillas de *Dacryodes chimantensis* y *Protium paniculatum* (Burseraceae) en un bosque de tierra firme de la amazonia colombiana. Desde diciembre de 1999 hasta junio de 2000 se registraron las visitas de frugívoros, la remoción de frutos y la dispersión primaria de semillas en 5 individuos por especie. Encontramos que *D. chimantensis* presenta en promedio una mayor altura, DAP, área de proyección de la copa y mayores cosechas que *P. paniculatum.* El porcentaje del valor promedio de frutos maduros de *D. chimantensis* osciló entre el 3 y el 21% del tamaño de la cosecha durante toda la estación de frutos, mientras que este porcentaje en *P. paniculatum* varió entre el 1 y 15%. Se observó actividad frugívora diurna en 4 de los 5 individuos de *D. chimantensis* estudiados, mientras que en los individuos de *P. paniculatum* no se presentó frugivoría diurna. Únicamente *Amazona festiva* y *A. amazonica* consumieron frutos de *D. chimantensis* y removieron en promedio 1.8 % de los frutos por árbol, pero no alejaron semillas viables del parental (dispersión primaria).

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En las trampas ubicadas bajo el área de la proyección de la copa sobre el suelo, encontramos que el número de frutos intactos, probados, y dañados por frugívoros fue similar para las dos especies. Las cosechas pequeñas, el número reducido de frutos maduros y las bajas tasas de reducción de la cosecha, sumado un bajo número de visitas, una baja remoción y dispersión primaria diurna de semillas por parte de los frugívoros, sugieren que estas dos especies tienen una dispersión limitada. Se discute el efecto de la baja dispersión por animales en los patrones de distribución espacial de estas especies.

Key words: Amazona*, Burseraceae, Colombian Amazonia, seed dispersal, Middle Caquetá River.*

4.1 INTRODUCTION

Seed dispersal is considered as one of the key processes determining the spatial structure of plant populations (Bleher and Böhning-Gaese 2001, Hubbell 1979, Nathan and Muller-Landau 2000, Schupp 1993). In tropical rain forests the role of animals in seed dispersal can be a critical factor influencing dynamics of plant recruitment (Bleher and Böhning-Gaese 2001, Connell 1971, Hubbell 1979, Janzen 1970, Jordano and Schupp 2000, Loiselle and Blake 1999), because more than 70% of plants have fruits adapted to attract fruit-eating animals (Foster *et al.* 1986, Frankie *et al.* 1974, Gentry 1982, Howe and Smallwood 1982, Howe and Westley 1988). Seed dispersal by animals includes a series of events from fruit removal up to patterns of seed deposition, including the transport of viable seeds away from the tree crown (primary dispersal), seed displacement from subsequent locations (secondary dispersal) and seed predation (Nathan and Muller-Landau 2000, Parrado-Rosselli *et al.* 2002, Schupp 1993, Wenny 2000b). Each of these events affects the survival and establishment success of seeds and seedlings (Connell 1971, Howe and Smallwood 1982, Howe and Westley 1988, Janzen 1970).

In the present study we evaluated primary seed dispersal of *Dacryodes chimantensis* Steyermark and Maguire (1967) and *Protium paniculatum* Engler (1942), two animal-dispersed Burseraceae species of terra firme rain forests in Colombian Amazonia, with clumped adult distribution patterns (A. Parrado-Rosselli unpublished data; see Chapter 5). Different authors have stated that frugivores might determine the abundance and spatial patterns of plant populations (Jordano and Schupp 2000, Loiselle and Blake 1999). Thus, based on the aggregated distribution pattern of these species, we expected to observe few visits, low fruit removal and limited primary seed dispersal on the part of animals feeding on their fruits.

4.2 STUDY SITE

The research was conducted at the Nonuya indigenous community of Peña Roja (0°39’05’’S, 72°04’45’’W), in the Middle Caquetá River region, State of Amazonas, Colombia. According to Holdridge *et al.* (1971) this region is classified as Humid Tropical Forest (bh-T). The study site is a terra firme rain forest of the Tertiary sedimentary plain (Duivenvoorden and Lips 1993). Mean annual temperature is 25.7°C and rainfall averages 3059 mm per year. Although the area does not have a marked dry season (months with less than 60 mm), rainfall decreases between December and February, while the highest levels occur between April and June.

4.3 STUDY SPECIES

D. chimantensis and *P. paniculatum* are dioecious canopy trees, fruiting every two years from December to June, with a peak of fruit ripening in May. Fruits of *D. chimantensis* and *P. paniculatum* are drupes, turpentine-like odorous, and generally single-seeded. Fruits and seeds of *D. chimantensis* are ellipsoid and larger-sized, heavier and with higher pulp percentage than the ovoid *P. paniculatum* fruits (Table 4.1). Fruits of both species have a thin exocarp, and a fleshy pulp. Fruits of *D. chimantensis* ripe from green-yellow to lustrous black; they are indehiscent with green pulp, while *P. paniculatum* fruits are dehiscent, green until maturity, with a white aril.

Table 4.1. Fruit characteristics of *Dacryodes chimantensis* and *Protium paniculatum* in a terra firme rain forest, Colombian Amazonia. Mean and standard deviations are based on measurements of 50 fruits and seeds per species.

	Dehiscence	Fruit size (cm)		Fruit mass (g)		Pulp		Seed size (cm)	
Tree species		Major diameter	Minor diameter	Wet	Dry	Type	%	Major diameter	Minor diameter
D. chimantensis	No	2.6 ± 0.1	1.4 ± 0.1	1.6 ± 0.2	0.6 ± 0.3	oily	28	2.2 ± 0.3	1.3 ± 0.1
P. paniculatum	Yes	1.6 ± 0.3	1.6 ± 0.3	1.4 ± 0.3	0.2 ± 0.0	juicy	19	1.5 ± 0.0	1.4 ± 0.1

Preliminary data of adult spatial distribution, showed that both species have a clumped pattern (*D. chimantensis* Eberhardt Index Ie = 1.55*;* *P. paniculatum* Ie = 1.32; Krebs 1989; A. Parrado-Rosselli unpublished data; see Chapter 5). *D chimantensis* fruits are consumed by indigenous peoples of the region, while *P. paniculatum* resin is used as incense, and as medicine for respiratory diseases.

4.4 METHODS

4.4.1 Data collection

From December 1999 to June 2000, frugivore visits, fruit removal and primary seed dispersal were recorded in five *D. chimantensis* trees, and five *P. paniculatum*. Trees were randomly selected along an existing trail system throughout a 95 ha area. Fruits of each species were characterised by measuring, weighing and describing a random sample of 50 fruits. Fruit and seed size was measured with callipers to the nearest 0.01 mm; and both major and minor diameter of fruits and seeds were considered. Wet and dry fruit weight was obtained to the nearest 0.1 g. Percentage of pulp was estimated as the difference between the major fruit and seed diameter. Vouchers of every tree individual were collected and determined at the Colombian Amazonic Herbarium (COAH).

We recorded diameter at breast height (dbh), tree height and area of canopy projection of every individual. Initial fruit crop size and the rate of fruit crop reduction of every tree were obtained through direct observations at the canopy level, which is considered a fairly accurate technique to estimate fruit quantity (Blake *et al.* 1990, Chapman *et al.* 1992, Zhang and Wang 1995; see Chapter 2). Thus, the approximate number of fruits at the beginning of the fruiting season could be estimated. To calculate initial fruit crop size we divided the fruit crown into 8 to 14 volumes, according to its size. We counted the number of unripe and ripe fruits in 3 out of these volumes selected on a random basis. Mean number of fruits of those 3 volumes was multiplied by the total estimated volumes of the fruit crown (Parrado-Rosselli *et al.* 2002). The fruit crop size reduction and the change in the number of unripe and ripe fruits throughout time were made through periodical counts of the same volumes every ten days until the end of each tree's fruiting season. The slope of the linear regression between time and the number of fruits counted every ten days was considered as the rate of fruit crop reduction (Parrado-Rosselli *et al.* 2002). Linear regressions also were made to obtain the rate of fruit ripening along the time.

4.4.2 Frugivory and animal activity

Observations were made at the canopy level from nearby trees to the focal individuals, providing accurate information on frugivory and primary seed dispersal than recordings carried out from the ground (Munn and Loiselle 1995, Parrado-Rosselli *et al.* 2002). Observations were made using binoculars (7X 35 mm), and canopy was accessed by single rope techniques. A total of 202 hours of observation was recorded for *D. chimantensis* and 133 for *P. paniculatum*. Each *D. chimantensis* tree was observed for a total of 40 hours, and each *P. paniculatum* 25 hours. Individual trees were observed 5 hours per day at different time intervals between 06:00 to 18:00 hours, alternating trees among days. No recordings were made during rainy days. Based on Parrado-Rosselli *et al.* (2002) we used two methods for evaluating animal activity in every tree. By conducting scan sampling of the tree crown every 15 minutes, we recorded animal species and number of individuals visiting the tree. Focal sampling (Martin and Bateson 1986) was used to record feeding behaviour of frugivores such as visit length, the number of fruits removed, dropped and damaged during a visit. Identification of frugivore species was made on the basis of Emmons and Feer (1990) and Hilty and Brown (1986).

4.4.3 Fruit traps

To complement our records on frugivory and fruit removal, we used 1 x 1-m fruit traps placed beneath the area of canopy projection of every tree studied. To cover 6% of the area of canopy projection (Howe 1982), the number of traps ranged from two to six. Fruit traps allowed to estimate fruit fall by factors different than diurnal frugivory such as rain, wind, and removal by evening and nocturnal animals. Traps were checked every 5 days, from the beginning to the end of the fruiting season. The number of fruits/seeds fallen into the traps were classified as intact (unripe and ripe), picked (removed parts of the pulp, with bill o tooth marks) and damaged (when seeds have been predated). For predated seeds we tried to identify the cause of death (*e.g.* larvae, rodents, birds). Each sampling period fruits and seeds were removed in order to exclude them from the next recording.

4.4.4 Data analysis

We used Spearman rank correlation to identify any relation between initial fruit crop size and the structural characteristics of trees, as well as to establish whether or not crop size and fruit production were associated with fruit crop reduction, frugivore visits and fruit removal by animals. To compare patterns of fruit ripening between individual trees we made Kruskal-Wallis analyses. Mann-Whitney tests were made to evaluate possible differences between the number of intact fruits, picked and damaged of *D. chimantensis* and *P. paniculatum.* All tests were performed based on Zar (1984) and Statistica (V.5.5 StatSoft 1999).

4.5 RESULTS

In general, *D. chimantensis* trees were taller than *P. paniculatum* trees (Table 4.2). Mean tree height, dbh, area of canopy projection, and initial fruit crop sizes of *D. chimantensis* were larger than in *P. paniculatum*. The initial fruit crop size of *D. chimantensis* was positively correlated with dbh (Spearman rank correlation $r_s = 0.90$, $P < 0.05$), and with the area of canopy projection ($r_s = 0.90$, $P < 0.05$). Fruit crop size, however, was not correlated with tree height ($r_s = 0.76$, $P > 0.05$). In *P. paniculatum* no significant correlations were found between initial fruit crop size and tree height, dbh, nor between initial fruit crop size and the area of canopy projection ($r_s = -0.42$, $r_s = -0.30$, $r_s = 0.6$, $P > 0.05$, respectively).

Table 4.2. Tree characteristics of *Dacryodes chimantensis* and *Protium paniculatum* in a terra firme rain forest, Colombian Amazonia. Mean and standard deviations are based on measurements of 5 individuals per species.

Tree species	Tree height (m)	dbh (cm)	Area of canopy projection (m^2)	Initial fruit crop size (No. fruits)
D. chimantensis	17.2 ± 1.8	29.5 ± 10.8	74 ± 30.2	216 - 5012
P. paniculatum	15.6 ± 0.7	17.2 ± 1.9	49.8 ± 5.3	330 - 2200

4.5.1 Fruiting and fruit crop reduction of *D. chimantensis* and *P. paniculatum*

During the study period (December 1999 – June 2000) mean percentage of ripe fruits of *D. chimantensis* relative to the fruit crop size ranged between 3 and 21% (Figure 4.1). The highest percentage of ripe fruits of *D. chimantensis* occurred in April. Ripe fruit production did not exhibited significant differences between individual *D. chimantensis* trees (Kruskal-Wallis analysis $H = 7.0$, $n = 42$, $K = 5$, $P < 0.05$). During the fruiting season of *P. paniculatum*, which occurred from December to April, mean percentage of ripe fruits oscillated between 1 and 15% (Figure 4.1). The highest percentages of ripe fruits were recorded in February and March. The percentage of ripe fruits did not show significant differences between individuals ($H = 8.39$, $n = 25$, $K = 5$, $P < 0.05$).

Fruit crop reduction in *D. chimantensis* trees ranged from 2 to 35 fruits per day (mean ± SE = 15 ± 5 fruits per day), while fruit crop reduction in *P. paniculatum* oscillated between 2 and 16 fruits per day. We found a significant positive correlation between fruit crop reduction and the number of ripe fruits ($r_s = 0.60$,

$P < 0.05$) in *D. chimantensis*, but not between fruit crop reduction and initial fruit crop size ($r_s = 0.88$, $P > 0.05$). Fruit crop reduction in *P. paniculatum* was positively correlated both with the initial fruit crop size ($r_s = 0.98$, $P < 0.05$) and with the number of ripe fruits in the tree ($r_s = 0.61$, $P = 0.05$).

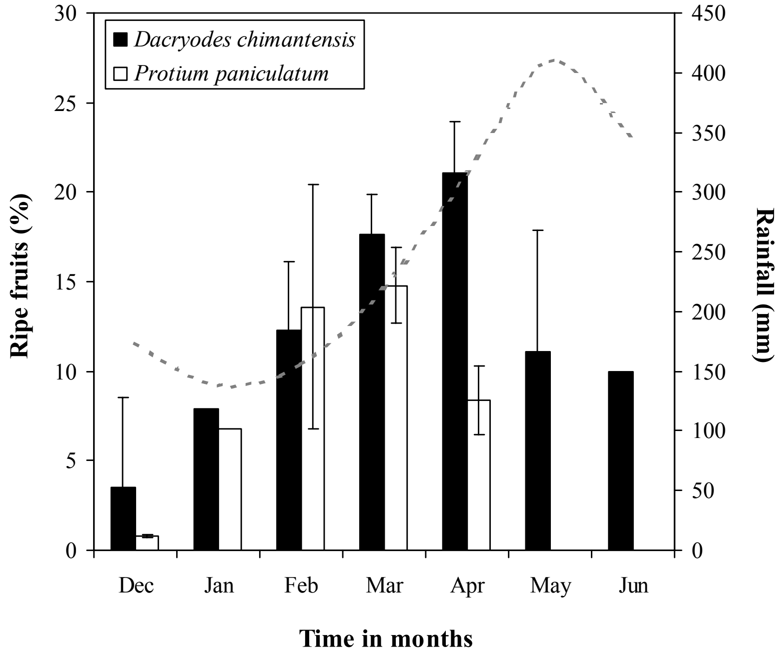

Figure 4.1. Mean percentage of ripe fruits relative to the fruit crop size of *Dacryodes chimantensis* and *Protium paniculatum* in a terra firme rain forest, Colombian Amazonia. Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.. No standard deviation is presented for June data of *D. chimantensis* as the fruiting season ended the first week of June.

4.5.2 Diurnal frugivory and fruit removal

Diurnal frugivore activity was observed in four out of the five *D. chimantensis* trees studied. Six species of birds visited *D. chimantensis* trees (Table 4.3). *Amazona fesitva* exhibited the highest number of observations (8). Only *A. amazonica* and *A. festiva* fed on the fruits of *D. chimantensis*. In contrast, no diurnal visits by frugivore or non-frugivore vertebrates were observed in any of the *P. paniculatum* trees.

Diurnal frugivores feeding on *D. chimantensis* fruits (*i.e. A. festiva* and *A. amazonica*) removed 16 ± 5 fruits per tree (1.8%) (*A. festiva* = 7 fruits; *A. amazonica* = 9 fruits). Fruit removal of *D. chimantensis* fruits was positively correlated with the proportion of ripe fruits in the tree ($r_s = 0.85$, $P < 0.05$). The number of frugivores per week was not correlated with the percentage of ripe fruits per week ($r_s = 0.24$, $P > 0.05$), neither the initial fruit crop size and the total number of frugivores observed in the tree ($r_s = 0.88$, $P > 0.05$). *A. festiva* and *A. amazonica* did not dispersed seeds of *D. chimantensis*. *A. festiva* dropped under the tree crown 33% of the seeds removed, and damaged 67%. *A. amazonica* dropped 18% and damaged 82%. Mean visit length of *A. amazonica* was 4.1 $\pm$ 1.8 min (Confidence limits 95% = 1.50–5.50 min), and mean feeding rate was 1.27 $\pm$ 0.4 fruits min^{-1} (Cl = 0-2 fruits min^{-1}). Mean visit length of *A. festiva* was 3.1 $\pm$ 1.2 min (Cl = 1.3-5 min), and mean feeding rate 1.64 $\pm$ 0.52 fruits min^{-1} (Cl = 0–2 fruits min^{-1}).

Table 4.3. Diurnal birds observed in the canopy of *Dacryodes chimantensis* trees in a terra firme rain forest, Colombian Amazonia. Number of visits and fruits removed in 5 individuals. Mean fruits removed per tree in parenthesis below (N = 4). Scientific names and order of species follows Hilty and Brown (1986).

Bird species			
Family	Species and common name	No. visits	No. fruits removed
Psittacidae	**Amazona festiva* (Festive parrot)	8	26 (7)
	**Amazona amazonica* (Orange-winged parrot)	6	35 (9)
Ramphastidae	*Ramphastos cuvieri* (Cuvier’s toucan)	1	0
Picidae	*Celeus elegans* (Chestnut woodpecker)	1	0
Thamnophilidae	*Myrmotherula* cf. *multiostrata* (Amazonian streaked-antwren)	1	0
Coerebidae	*Cyanerpes caeruleus* (Purple honey creeper)	2	0
	TOTAL	19	61

* Predators (*sensu* Snow 1981)

4.5.3 Fruit traps

The fruit traps located under the area of canopy projection showed that 43.0% of *D. chimantensis* fruits were picked by vertebrates (parrots, rodents and primates). The percentage of intact fruits was 35.8%, while 21.2% exhibited predated seeds (Figure 4.2). Birds (parrots) accounted for 6.8% of the seeds predated, 4.7% were predated by invertebrate larvae, and 9.7% by rodents. Regarding *P. paniculatum* 39.0% of the fruits found in the traps had been handled by parrots, rodents, primates, bats, and ants, while 41.7% were intact fruits. Of the seeds predated (19.3%), 7.5% were damaged by invertebrates while 11% were damaged by vertebrates. The number of intact, picked and damaged fruits found in the traps was similar for both species (Mann-Whitney $U_{5,5} = 13$, $P < 0.05$, $U_{5,5} = 5$, $P < 0.05$, $U_{5,5} = 20$, $P = 0.05$, respectively). None of the two species showed a significant correlation between the number of picked fruits and fruit crop size (*D. chimantensis* $r_s = 0.8$, $P > 0.05$; *P. paniculatum* $r_s = 0.56$, $P > 0.05$).

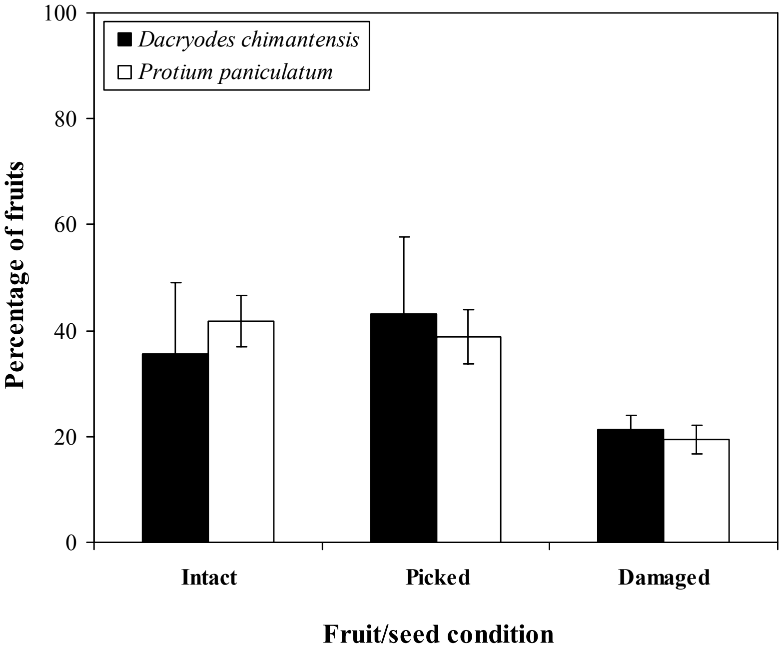

Figure 4.2. Mean percentage of intact, picked and damaged fruits (undispersed) of *Dacryodes chimantensis* and *Protium paniculatum* found in the fruit traps located beneath the tree crown in a terra firme rain forest, Colombian Amazonia.

4.6 DISCUSSION

Results found in the this study suggest that *D. chimantensis* and *P. paniculatum* might be dispersal limited. Although *D. chimantensis* showed diurnal frugivory in contrast to *P. paniculatum,* it was lower than other studies on frugivory and fruit removal of tropical rain forest tree species (see Bleher and Böhning-Gaese 2001, Böhning-Gaese *et al.* 1995, Howe 1982, Parrado-Rosselli *et al.* 2002), and lower than studies that have reported the genera *Dacryodes* and *Protium* in the diets of tropical frugivores (Defler and Defler 1996, Gautier-Hion *et al.* 1985, Stevenson *et al.* 2000, Stevenson *et al.* 2002). Besides, only the parrots *A. festiva* and *A. amazonica* removed seeds from the parent tree, but destroyed and/or dropped all fruits removed.

Fruit crop sizes and fruiting patterns also impose limitations to seed dispersal. *D. chimantensis* and *P. paniculatum* exhibited small fruit crop sizes, with a low proportion of ripe fruits that never surpassed 21% of the fruit crop size. The low ripe fruit availability coincided with the highest number of species fruiting at the community level, that occurred from the late dry season until mid wet season (see Chapter 3). Therefore, during *D. chimantensis* and *P. paniculatum* fruiting season, species with higher number of fruiting individuals and larger crops such as *Protium altsonii*, *P. pilosum*, *P. polybotryum* and *Clusia* spp. (see Chapter 3) could have been more attractive for frugivores. Consequently, the low ripe fruit availability of both species during their entire fruiting season compared to the high availability of fruits in the forest, might explain the limited number of diurnal frugivores. Moreover, preliminary studies on the local fauna indicated that animal density in the Tertiary sedimentary plain is low in comparison with nearby ecosystems (Cuadros 1993, Sarmiento 1998). Therefore, during the fruiting peaks of the forests, the few dispersers would select for other species with larger crops, as they are more attractive and tend to be preferred than plant species with smaller crops (Howe and Estabrook 1977, Nathan and Muller-Landau 2000, Snow 1971). Although in our study area hunting is the most common source of animal protein for indigenous peoples, we do not think it could significantly affect the seed dispersal processes of both *D. chimantensis* and *P. paniculatum*. The Tertiary sedimentary plain forests are rather used for hunting, and bird consumption is merely casual (Sarmiento 1998). Even more, some studies have stated that occasional hunting no necessarily lead to animal extinction or alteration of the plant-animal interactions; instead it can be conceived as a mechanism for maintaining animal populations (Roldan and Simonetti 2001, Winterhalder and Lu 1997). This can be happening in our study site where subsistence hunting is a millenary activity (Sarmiento 1998).

A limited diurnal primary seed dispersal not necessarily implies lack of dispersal. For example, picked and damaged fruits of *P. paniculatum* found in the traps suggest that most of the fruit consumption occurs during the night probably by bats and non-flying mammals, which might be carrying some of seeds away from the parent tree. However, based on the low rate of fruit crop reduction this percentage does not seem to be very high. Nocturnal fruit consumption is also supported by the dispersal syndrome of *P. paniculatum*. The green fruit coat combined with a white aril, its characteristic odour, and its fruiting patterns seem to be typical for bat-dispersal (Fleming 1979, Heithaus *et al.* 1975, Howe 1982, Korine *et al.* 2000, Van der Pijl 1982). Some studies also have reported fruit consumption of the genus *Protium* by bats and non-flying mammals (Brooks *et al.* 1997, Miller and Miller 2003, Stevenson *et al.* 2002). Other studies have also recorded fruits and seeds of the genera *Dacryodes* and *Protium* in the diets of oilbirds (*Steatornis caripensis*; Snow 1962). Thus, in the study area the oilbird might be a potential seed disperser of these species due to its nocturnal foraging habits, and seasonal gregarious movements between habitats in search for food (Hilty and Brown 1986). Although diurnal frugivory was not found in *P. paniculatum*, and rate of fruit crop reduction was lower than *D. chimantensis*, percentages and marks on picked and damaged fruits found in the traps, suggest that the amount of fruits removed in both species is similar, and that they might be sharing frugivores such as rodents, bats, primates and ants. Probably, effective primary seed dispersal occurs during occasional, casual or opportunistic visits by birds or mammals. For instance, during casual observations we recorded the bird species *Penelope jacquacu*, *Pionites melanocephala* and *Ramphastos cuvieri,* and the primate species *Saguinus fuscicollis* feeding on the fruits of *D. chimantensis*. The latter were also seen feeding on *P. paniculatum* fruits. Probably, the researcher presence in the canopy could have influenced frugivore visits. Although this event does not seem to occur with birds (Parrado-Rosselli *et al.* 2002), we noticed that observer presence affected primates, which responded by changing their foraging routes and feeding rates. Opportunistic visits by frugivores may be contribute to primary seed dispersal, because few fruits in a faecal aggregate diminishes risks of predation while probability of germination increases (Jordano 1992, Wenny 2000a). Parrots and macaws (Psittacidae), usually considered seed predators, also may be carrying seeds away from the tree crown either by ingestion or by accidental transport (Bleher and Böhning- Gaese 2001, Böhning-Gaese *et al.* 1995, Böhning-Gaese *et al.* 1999, Parrado-Rosselli *et al.* 2002). However, frugivore feeding behaviour, and their role as seed dispersers change between species (Jordano and Schupp 2000). A larger sample size, nocturnal observations and a detailed characterisation of the seed shadow would be important for validating these ideas.

In spite of a limited diurnal seed dispersal, recruitment of both *D. chimantensis* and *P. paniculatum* may be enhanced by their fruiting patterns. Both species fruited from the dry season until wet season, which seems to coincide with appropriate climate conditions for the dehiscence of *P. paniculatum* fruits and for seed germination (Garwood 1982, Gautier-Hion 1990). The highest amount of *P. paniculatum* ripe fruits was found at the end of the dry season, when atmosphere conditions enhance desiccation of the fruit coat. The fleshy *D. chimantensis* indehiscent drupes tend to ripe during the peak of the wet season, which enhances seed germination (Garwood 1982). On the other hand, a simultaneous study in the same area, about survival and distribution pattern of *D. chimantensis* seeds, Londoño (2000) found a higher proportion of viable seeds under and near the tree crown. Probably as a response to the seed dispersal limitations, the two species have developed higher survival capacity in the vicinity of the parent tree, where environmental conditions as soil drainage and irradiance are more homogeneous; hence, seedling and juvenile establishment might be enhanced (Bustamante and Simonetti 2000, Forget *et al.* 1999, Hubbel 1980). It would be important to evaluate secondary dispersal and post-dispersal events in order to find out successful establishment of dispersed and non dispersed seeds (Schupp 1993), and whether or not fruiting seasonality affects germination success of both species.

Even though it is necessary to correlate frugivore activity and seed dispersal with the spatial distribution pattern of seedlings and adults (Bleher and Böhning-Gaese 2001, Connell 1971, Hubbell 1979, Janzen 1970), we consider that one of the factors that can generate the aggregated distribution pattern of *D. chimantensis* and *P. paniculatum* in the study area (A. Parrado-Rosselli unpublished data; see Chapter 5) is the low diurnal seed dispersal. Thus, the seeds deposited under and in the vicinity of the parent tree could be enriching the present patch, while the few seeds dispersed are sufficient to explain the creation of a new patch. Although our sample size of is too small to obtain definitive conclusions, the high number of observation hours, and other biological facts support our findings. Long term research about post primary seed dispersal stages should be the focus of future studies. Thus, if seed dispersal is affecting population structure of these Amazonian tree species, the deviations between seed and seedling shadows and adult distributions are expected to be low (see Chapter 5).

5. EFFECT OF SEED DISPERSAL ON SPATIAL DISTRIBUTION PATTERNS OF COMMON TREE SPECIES IN A TERRA FIRME RAIN FOREST OF COLOMBIAN AMAZONIA

Parrado-Rosselli, A.

ABSTRACT

The effect of seed dispersal by animals on the patterns of spatial distribution of *Dacryodes chimantensis* (Burseraceae) and *Brosimum utile* (Moraceae), two common tree species of terra firme rain forests in Colombian Amazonia was evaluated. Animal seed dispersers and patterns of seed deposition by frugivores were recorded for each tree species. The spatial patterns of seed, seedling and sapling distribution relative to parent trees were obtained. In addition, the density and spatial distribution of juveniles (1 – 9.99 cm dbh) and adult trees (> 10 cm dbh) were recorded throughout a 95 ha area. The results showed that frugivore activity and seed dispersal by vertebrates was higher and more efficient in *Brosimum* than in *Dacryodes* in terms of the number of animal dispersers, the quantity and quality of their feeding behaviours, and the number of seeds transported away from the parent tree. Tamarins, toucans, and rodents were the main dispersers of *Brosimum* seeds, while no particular species or set of frugivores dispersed *Dacryodes* seeds. Dispersal distances of *Dacryodes* seeds, seedlings, saplings away from the parent tree (range: 6.2 – 14.5 m) were consistent with distances of seed deposition by animals (birds = 5.1 – 8.6 m; mammals = 4.9 – 8.3 m), and with the mean nearest neighbour distance of juveniles (10.9 m) and adults (15.4 m). Both *Dacryodes* juveniles and adults exhibited a clumped distribution pattern, with more than 50% of individuals being within 15 m of each other. Dispersal distances of *Brosimum* seeds, seedlings and saplings (11.0 – 21.5 m) corresponded well with distances of seed deposition by birds (8.9 – 14.0 m) and mammals (14.1 – 18.2 m), with the random distribution pattern and nearest neighbour distances of juveniles (20.2 m) and adults (25.2 m). The results presented here showed that on the local scale, the low dispersal *Dacryodes* was correlated with a clumped tree population, whereas the high seed dispersal of *Brosimum* was correlated with a randomly distributed tree population. The combined effect of the type of frugivores, their feeding behaviours, and the seed displacement by all seed dispersal agents seem to be the most likely explanation for the observed spatial patterns of common tree species in the terra firme rain forests of Colombian Amazonia.

RESUMEN

Se evaluó el efecto de la dispersión de semillas por animales en los patrones de distribución espacial de *Dacryodes chimantensis* (Burseraceae) y *Brosimum utile* (Moraceae), dos especies de árboles comunes en los bosques de tierra firme de la amazonia colombiana. Para cada una de las especies se registraron los dispersores de semillas y los patrones de deposición de semillas por frugívoros. También se obtuvo la distribución espacial de las semillas y plántulas respecto a los árboles parentales, así como la densidad y la distribución espacial de los juveniles (1–9.99 cm dap) y adultos ($\geq$ 10 cm dap) en un área de 95 ha. Los resultados muestran que la actividad frugívora y la dispersión de semillas por vertebrados fue más alta y más eficiente en

Brosimum que en *Dacryodes* en términos del número de agentes dispersores, la cantidad y la calidad de sus comportamientos alimenticios, y el número de semillas alejadas del parental. Los tamarinos, tucanes, y roedores fueron los principales dispersores de semillas de *Brosimum,* mientras que no se registraron frugívoros dispersando las semillas de *Dacryodes.* Las distancias de dispersión de las semillas y plántulas de *Dacryodes* respecto al parental (rango: 6.2 – 14.5 m) correspondieron con las distancias de deposición de semillas por animales (aves = 5.1–8.6 m; mamíferos = 4.9–8.3 m), y con la distancia media al vecino mas cercano de juveniles (10.9 m) y adultos (15.4 m). Los adultos y juveniles de *Dacryodes* presentaron un patrón de distribución agregado, con más del 50% de los individuos concentrados a 15 m uno del otro. Las distancias de dispersión de las semillas y plántulas de *Brosimum* concordaron con las distancias de deposición de semillas por aves (8.9–14.0 m) y mamíferos (14.1–18.2 m), con la distribución al azar y las distancias al vecino mas cercano de juveniles (20.2 m) y adultos (25.2 m). Los resultados aquí presentados muestran que a una escala local, la baja dispersión de semillas de *Dacryodes* estuvo correlacionada con la distribución agregada de los árboles en la población, mientras que la alta dispersión de semillas de *Brosimum* estuvo correlacionada con la distribución azarosa de los árboles en la población. El efecto combinado del tipo de frugívoros, su comportamiento alimenticio, y el desplazamiento de semillas por los agentes dispersores parece ser la explicación más apropiada para explicar los patrones observados de la distribución espacial de especies comunes de los bosques de tierra firme de la amazonia colombiana.

Key words: Brosimum utile, Dacryodes chimantensis, *Middle Caquetá River region, seed dispersal, seed shadow, seedling shadow, spatial pattern, tropical rain forest*

5.1 INTRODUCTION

Several studies have been focused on the factors that influence the diversity and spatial distribution patterns of plant species in tropical rainforests (*e.g.* Clark *et al.* 1998, Duivenvoorden 1995, 1996; Duque 2004, Duque *et al.* 2003, Hubbell 1998, Hubbell and Foster 1986, Pitman *et al.* 1999, Svenning 2000, Terborgh and Andresen 1998, Tuomisto *et al.* 2002). Diverse factors have been proposed based on abiotic or biotic processes, and at local or greater spatial scales (Duivenvoorden *et al.* 2002, Duque 2004, Duque *et al.* 2003, Terborgh *et al.* 2002). Among these factors, seed dispersal is known to influence the recruitment and demography of plant populations, particularly on a local meso-scale (Herrera *et al.* 1994, Hubbell 1979, Nathan and Muller-Landau 2000, Schupp 1990, Wenny 2000b).

Seed dispersal by animals, including seed predation and seedling establishment, is crucial for understanding the regeneration dynamics of populations and communities (Bleher and Böhning-Gaese 2001, Forget *et al.* 1998, Fragoso 1997, Herrera *et al.* 1994, Hubbell 1979, Nathan and Muller-Landau 2000, Schupp 1990, Schupp *et al.* 2002, Silva-Matos and Watkinson 1998, Wenny 2000b). Seed dispersal is particularly important in tropical rain forests where most of the plants have fruits adapted for animal dispersal (Howe and Smallwood 1982). Feeding behaviour and foraging patterns of fruit eating animals are largely species-specific, and vary widely, even between closely allied animal species (Jordano and Schupp 2000, Schupp 1993). Feeding behaviours are influenced both by the morphological characteristics of frugivores, and by plants attributes such as fruit and seed size, fruiting patterns, and by the availability of other fruit resources in the community (Altrichter *et al.* 2002, Di Fiore 2003, Forget *et al.* 2002, Galetti and Aleixo 1998, Henry 1999, Parrado-Rosselli *et al.* 2002, Peres 1994, Silvius and Fragoso 2003, Stevenson *et al.* 2000, Wenny 2000b). Therefore, to assess whether fruit consumption influences the number and the spatial patterns of viable seeds that reach the soil depends largely on the evaluation of plant features, and the feeding behaviour of the frugivores when visiting a fruiting tree (*e.g.* frequency of visits, fruit handling, feeding rates, fruit removal, transport of seeds away from the parent tree, the effects of gut treatment on germination, and post-feeding movements of animals; Jordano and Schupp 2000, Loiselle and Blake 1999, Schupp 1993, Wenny 2000b).

In the terra firme rain forests of the Middle Caquetá River Region, in Colombian Amazonia, as elsewhere in the tropics, 81% of the tree species have fruits adapted for animal dispersal (Castaño-A 2003). In addition, studies carried out in this region have found that within terra firme rain forests variations in soil fertility explain only a fraction of the observed patterns in plant distribution (Duivenvoorden 1995, 1996; Duque 2004, Duque *et al.* 2003). Consequently, other factors such as seed dispersal processes, may also affect the spatial distribution of plants. In order to understand the effect of seed dispersal by animals on the patterns of distribution and space occupation of tree species of this region of Colombian Amazonia, the main question of this paper was to evaluate whether seed dispersal processes, (including type and feeding behaviour of frugivorous animals, seed predation and seedling establishment) of common animal-dispersed tree species, with regular, predictable and synchronous fruiting patterns, are shaping the observed patterns of spatial distribution of juveniles and adults in the community (local-scale). To answer this question, *Dacryodes chimantensis* (Burseraceae) and *Brosimum utile* (Moraceae), two common tree species of terra firme rain forests of this region of Colombian Amazonia (Duivenvoorden and Lips 1993; see Appendix 1) were selected, since preliminary observations indicated that they have contrasting distribution patterns. While *Dacryodes* trees seem to be clustered into fairly discrete natural groves, the spatial distribution of *Brosimum* trees seems to depart from a clustered pattern. Common species were selected since rare species are more recruitment-limited, and other and unknown processes of mortality and survival of seeds and seedlings may be involved (Schupp *et al.* 2002). Moreover, the study of species with regular and seasonal fruiting patterns can provide better information on the plant features that cause a differential exploitation by frugivores. It is, therefore, hypothesised that the clumped distribution of *Dacryodes* trees is the consequence of a low animal activity, low fruit consumption, low seed dispersal, and short seed dispersal distances from parent trees. The randomly spaced populations of *Brosimum*, are proposed to be the result of higher visitation rates, higher seed dispersal by animals, and more seeds transported at longer distances away from the parent tree.

5.2 STUDY SITE

The field work was carried out in a terra firme rain forest of the Tertiary sedimentary plain (TSP) in the vicinity of the indigenous community Nonuya of Peña Roja, in the Middle Caquetá River region, State of Amazonas, Colombia (0°39’05’’S, 72°04’45’’W). Mean annual rainfall is 3060 mm, with a moderate dry season from December to February, while May and June are the wettest months (Duivenvoorden and Lips 1993). The TSP is the most extensive of the four broad landscape units recognised in the Middle Caquetá River region (Duivenvoorden and Lips 1993). Dominant plant families in the study site include Mimosaceae, Fabaceae, Lecythidaceae, Arecaceae and Dipterocarpaceae (Castaño-A 2003, Londoño-Vega and Alvarez-Dávila 1997; see Appendix 1 and Chapter 1 for detailed descriptions).

5.3 STUDIED TREE SPECIES

Dacryodes chimantensis Steyermark and Maguire (1967) (Burseraceae) (henceforth *Dacryodes*), is found in tropical humid and lower montane forests below 1800 m elevation. This species is a dioecious mid-storey and overstorey tree of terra firme rain forests of North-west Amazonia (Ecuador, Perú, Venezuela, and Colombia). In the Middle Caquetá River Region, the *laurel de perico* (local name) is very abundant and observed mainly on nutrient-poor, well drained soils (Duivenvoorden and Lips 1993, Londoño-Vega and Alvarez-Dávila 1997). Its fruits are indehiscent single-seeded drupes, turpentine-like odorous, ellipsoid with a major diameter of 26 ± 1 mm (mean ± SD), and a minor diameter of 14 ± 1 mm (n = 50). Individual dry fruit weight is 0.6 ± 0.3 g (n = 50). Fruits mature from green to yellow, and its seeds are on average 22 ± 3 mm x 13 ± 1 mm in size (n = 50). *Dacryodes* fruits are characterised by an oily resinous mesocarp which is known for providing a significant fraction of the diet of specialised frugivorous birds (*e.g. Steatornis*; Snow 1962). *Dacryodes* plays an important role in the ethnobotany of indigenous communities of the area. The buds are used to heal scorpion bites and the resin (incense) is used for illumination, rituals, protection against demons, diseases, bites from scorpions and snakes and as medicine for respiratory diseases.

Brosimum utile Kunth (1846) (henceforth *Brosimum*), known as milk tree, sande, vaco, baco or lechoso, is an important timber-producing species of the Moraceae family. This species is widespread in northern South America and in part of Central America, mainly found in tropical humid and pre-montane forests below 900 m. The Amazonian subspecies, *Brosimum utile* subsp. *ovatifolium* (Ducke) C.C. Berg (1970), is distributed along the Amazonian basin in Colombia, Ecuador and Perú, and western Brazil. It is a dioecious canopy tree, very abundant and generally found in nutrient poor, well-drained soils of the Middle Caquetá River Region (Duivenvoorden and Lips 1993, Londoño-Vega and Alvarez-Dávila 1997). Females produce fleshy spherical one-seeded drupes (15 ± 1 mm x 12 ± 1 mm in size; n = 50), succulent, brown-coloured, sweet-tasting, edible when mature and weighting 0.6 ± 0.1 g (dry fruit weight, n = 50). Seeds are spherical (0.41 ± 0.04 mm) and covered by a thin brown pericarp. Fruits and seeds are attractive to many species of birds, primates and ground-mammals, particularly small rodents and spiny rats (Janzen 1991, Stevenson *et al.* 2000). Wood of *Brosimum* is medium-dense, generally used for light constructions and interiors. The latex has a medicinal use, to stick feathers to the body during rituals, as well as it is used in the mixture for caulking canoes. From the bark, indigenous peoples make a bag for carrying *mambe* (coca powder) and clothes for rituals.

5.4 METHODS

5.4.1 Fruiting phenology

The examination of herbarium collections (Borchert 1996) of Colombian Amazonia (Colombian Amazonic Herbarium – COAH and Colombian National Herbarium –

COL) indicated that *Dacryodes* bears fruit supra-annually (every two or three years), and *Brosimum* sub-annually (twice a year). However, in order to obtain actual patterns of fruit production of both species, 16 female *Dacryodes* trees and 10 of *Brosimum* distributed throughout a 95 ha area were monitored once a month to assess their fruiting phenology. The presence and number of fruits in *Dacryodes* trees were monitored over 33 months, from January 2000 to September 2002, while *Brosimum* was monitored over 27 months, from June 2000 to September 2002. For each plant individual, the number of fruits was calculated by counting the number of fruits in 3 randomly selected volumes of same size of the fruit crown (see Chapter 2). The mean number of fruits of those three volumes was multiplied by the total estimated volumes of the fruit crown. Fruiting patterns, measured as the number of fruits, were compared with simultaneous data on community wide fruiting (see Chapter 3). Fruiting pattern of each species was assigned into one of three duration classes (*i.e.* brief fruiting < 1 mo; intermediate fruiting 1 to 5 mo; extended fruiting > 5 mo) and frequency classes (*i.e.* sub-annual < 12 mo; annual = 12 mo; supra-annual > 12 mo; Chapman *et al.* 1999, Newstrom *et al.* 1994; see Chapter 3). Vouchers of each individual were collected, and were determined in the Colombian Amazonic Herbarium (COAH), in Bogotá, Colombia.

5.4.2 Frugivory and primary seed dispersal

Of the individuals selected for phenological records, a set of five trees per species was randomly selected for the study (during a single fruiting season) of frugivory, seed dispersal, the spatial patterns of seed, seedling and sapling distribution relative to parent trees (henceforth seed, seedling and sapling shadows, respectively; Jordano and Godoy 2002). Selected *Brosimum* trees were on average taller and with larger crops than *Dacryodes* trees (Table 5.1). Estimated mean initial fruit crop sizes were 16620 fruits per tree in *Brosimum* (range 5600 – 39800 fruits) and 1608 fruits per tree in *Dacryodes* (range 216 – 5012 fruits). During the reproductive event studied no abortion was detected for *Dacryodes* while the number of fruits of *Brosimum* was reduced by abortion to about 40.9 (± 8.5)% fruits per tree.

Table 5.1. Characteristics of *Dacryodes chimantensis* and *Brosimum utile* trees (n = 5 per species) in a terra firme rain forest, Colombian Amazonia. Mean and standard deviation of tree height, diameter at breast height (dbh) and area of canopy projection. The order of the species in the tables follows Cronquist (1981).

Tree species	Height (m)	dbh (cm)	Area of canopy projection (m^2)
D. chimantensis	17.2 ± 1.8	29.5 ± 10.8	74 ± 30.2
B. utile	30.0 ± 5.2	40.7 ± 18.5	135.0 ± 32.4

Frugivore visits, fruit removal in the tree crown and primary seed dispersal (*i.e.* dispersal by arboreal and/or flying animals directly in the fruiting tree crown), of *Dacryodes* trees were recorded for a total of 202 hours from January to June 2000

(Rozo-Mora and Parrado-Rosselli 2004; see Chapter 4). *Brosimum* trees were observed for 90 hours between March and April 2002. Recordings were made at different time intervals between 06:00 to 18:00 hours, alternating trees between days. Observations were made using binoculars (7X 35 mm and 8X 40 mm), and were carried out at the canopy level from a nearby tree accessed by single rope techniques. All vertebrate species visiting the tree were recorded. Focal sampling (Martin and Bateson 1986) was used to obtain the length of feeding visits, the number of fruits removed, dropped and damaged during a visit, and feeding rates (Parrado-Rosselli *et al.* 2002). Repeated visits by the same animal were treated in the same manner as visits by different animals.

5.4.3 Seed deposition by frugivores

Seed deposition by frugivores was evaluated by collecting fruits handled by animals in forty 1 x 1-m plots set out every 5 m, along the 4 cardinal directions from the base of the parent tree. This complemented observations on diurnal frugivory and seed dispersal, allowing the identification of possible nocturnal and secondary seed dispersers (*i.e.* terrestrial dispersers following primary dispersers as arboreal and/or flying animals). Plots were checked three times a week during the entire fruiting season of each species. The number of fruits/seeds handled by animals was counted at each visit. Handled fruits/seeds were classified as all fruits with picked or removed parts of the pulp, with bill or tooth marks, regurgitated, defecated or predated by birds or mammals. Handled fruits/seeds were classified into bird-handled or mammal-handled. The total percentage of fruits handled per tree species and the number of fruits handled per m^2 each 5 m were obtained.

5.4.4 Seed and seedling shadow

The spatial pattern of seed and seedling distribution was evaluated within 0-50 m distance from the base of the same five trees per species studied. For the seed shadows, seed density was estimated in 1 x 1-m plots every 5 m along four 50 m transect radiation from the base of the parent plant. Seed shadows were evaluated at the end of each tree's fruiting season, when considerable post-dispersal removal, secondary dispersal, and hence, seed rearrangement had already occurred (Sánchez-Cordero and Martínez-Gallardo 1998). Seeds found in each plot were classified into viable or predated. The cause of death (*i.e.* vertebrate, invertebrate larvae and bruchid beetles-, fungal pathogens) was determined by examining if predated seeds were peaked, with beak marks, shredded in to pieces, with insect larva, pupa, and/or adult exit hole.

Patterns of seedling and sapling distribution were estimated along the whole length of same four 1 x 50-m radial transects described above. Recordings were conducted three months after the end of each species fruiting season, which was considered the peak of the seedling establishment process. All seedlings ≤ 1 cm dbh found in these transects were identified, marked, and classified into one-year seedlings (henceforth seedlings) and saplings. Seedlings were newly established (*i.e.* first year) while saplings were older than 1 year (Hladik and Mitja 1996). *Dacryodes* seedlings (< 1 y) were below a height of 25 cm (range 13 – 24 cm; n = 22), and saplings below 50 cm (range 25 – 50 cm; n = 14). *Brosimum* seedlings (< 1 y) were below 35 cm height (range 20 – 32 cm; n = 15), and saplings were below a height of 70 cm (range 41 – 68 cm; n = 9).

Actual seedling/sapling mortality could not be evaluated because only one census at a single point in time was made. Therefore, seedling and sapling damage were assessed as indicators of *potential* death. Causes of potential predation were classified as herbivores (vertebrates and/or invertebrates), and disease (lifeless, burned-like and discoloured leaves by fungal pathogens or other undetermined disease). If one or more leaves of seedlings/sapling showed such damage, it was classified as attacked by predators.

5.4.5 Density and spatial distribution of species

Density and spatial distribution of *Dacryodes* and *Brosimum* juveniles (1–9.99 cm dbh) and adult trees (> 10 cm dbh) were assessed through plot-based censuses. Transect based censuses were also made, but were only possible for *Brosimum*. In three 1-ha plots and six 0.25-ha plots, all *Dacryodes* and *Brosimum* individuals $\geq$ 1 cm dbh found within the plot boundary were censused and marked. Plots were randomly located throughout a 95 ha area. Searches of *Dacryodes* and *Brosimum* within the plot were conducted by the author, two students and three indigenous field assistants. Each individual was mapped to the nearest 0.5 m using a Suunto compass, 50 m tape, and trail grids (10 x 10-m) covering the entire plot. The *Brosimum* transect censuses were conducted along two transects of 10-m x 2-km each. Each *Brosimum* individual $\geq$ 1 cm dbh within the transect was counted and marked. Additionally, the distance along the transect and the perpendicular distance to the transect centre were recorded. All individuals recorded in each plot were collected and determined at the Colombian Amazonic Herbarium (COAH), in Bogotá, Colombia.

5.4.6 Data analysis

Seed removal success (Jordano and Schupp 2000) was measured as the number of fruits/seeds removed (taken) by frugivores. Dispersal success (Jordano and Schupp 2000) was estimated as the number of seeds leaving the tree crown (seeds carried away) through the activity of frugivores (Parrado-Rosselli *et al.* 2002). The number of seeds carried away was calculated as the difference between the number of fruits removed by animals minus the seeds dropped and damaged before being swallowed. Regurgitated seeds and those swallowed when the animal defecated on the tree after visits longer than 15 minutes were also discounted (Parrado-Rosselli *et al.* 2002). Seeds transported in animal hands, beaks, and legs were also considered as carried away. Seeds carried away were expressed as a percentage relative to the total seeds removed by animals (Parrado-Rosselli *et al.* 2002).

Although some seeds and seedlings recorded may originate from different parent trees, the seed and seedling transects based on the 5 females per species were believed to contain seed or seedlings exclusively from those parent trees, with the closest trees being males or not bearing fruit during the study period.

Skewness and kurtosis were calculated for the seed, seedling and sapling shadows. Kurtosis was used to measure the degree of flatness or peakedness of the distribution of seeds/seedlings/saplings (Sokal and Rohlf 1980). The ratio of kurtosis to its standard error was used as a test of normality (normality is rejected if the ratio is less than –2 or greater than +2). A large positive value indicates that the distribution peaks more and has longer tail than the normal distribution, and negative if it is flatter. Skewness was used to describe whether seed/seedling/sapling distributions were biased near or far from the parent tree. The ratio of skewness to its standard error was used as a test of normality (normality is rejected if the ratio is less than –2 or greater than +2). A positive value indicated that the number of seeds/seedlings/saplings peaked nearer the parent tree than the peak of a statistically normal distribution, and negative if it peak occurred further away (Sokal and Rohlf 1980).

The probability of transition of seeds to the seedling stage, and of seedlings to the sapling stage for each distance class was measured as the ratio of seedlings established per falling seed for each distance class, and the ratio of saplings recorded per established seedling. Spearman rank correlations were used to assess whether patterns of predation of seeds, seedlings and saplings were a function of distance from parent tree or a function of density of seed, seedlings or saplings. Spearman rank correlations were also used to examine spatial consistency between life stages.

Several methods have been developed to analyse and characterise the density and spatial patterns of plants (see Krebs 1989). Amongst density methods, the Diggle's estimator of population density was used for the plot-based censuses, and the uniform model with cosine function adjustments (Buckley *et al.* 1993) for the transect-based censuses. Density estimates for adult trees (> 10 cm dbh) were made independently from juveniles (1 – 9.99 cm dbh). To obtain spatial distribution patterns of adult trees and juveniles the Donnelly index of aggregation (Donnelly 1978) and the Hopkins' test statistic for randomness (Hopkins 1954) were used. The Donnelly index of aggregation is a modification of the Clark and Evans test (1954) where observed nearest neighbour distances of *Dacryodes* and *Brosimum* for each age category (*i.e.* adults and juveniles) were tested against the expected distances to nearest neighbour corrected for lack of a boundary strip. The Hopkins' test is distributed as F with 2n degrees of freedom in the numerator and the same in the denominator. Thus, the F-test for h is a two-tailed F-test in which the null hypothesis of randomness will be accepted if h is within F-values range; rejected in favour of a uniform pattern if observed h is less than $F_{0.025,\ 2n,\ 2n}$ and rejected in favour of a clumped pattern if observed h is greater than $F_{0.975,\ 2n,\ 2n}$. For the transect method, the distribution of *Brosimum* juveniles and adults was examined using the number of trees detected along each transect segment of 100 m. All tests were performed based on Zar (1984), Statistica (V.5.5 StatSoft 1999) and Distance (V.4. Thomas *et al.* 2002).

5.5 RESULTS

5.5.1 Fruiting phenology

Dacryodes and *Brosimum* showed fruiting seasonality, but exhibited contrasting fruiting patterns both in duration and frequency (Figure 5.1). *Dacryodes* fruit production was extended (> 5 mo), supra-annual (2 y), and peaked when fruit available in forest was at their maximum (Figure 5.1). Duration of *Brosimum* fruiting was intermediate (1 to 5 mo), and fruited sub-annually (6 mo approx.). The number of *Brosimum* fruits varied widely among years. Major fruit production of *Brosimum* occurred in 2002, during the highest number of fruits ha^{-1} recorded at the forest site (Figure 5.1). Mean percentage of *Dacryodes* ripe fruits mo^{-1} was low but relatively constant throughout time (mean ± SD = 11.9 ± 1.8% fruits mo^{-1}), while mean percentage of ripe fruits of *Brosimum* mo^{-1} was higher but more clumped in time (39.0 ± 19.7% fruits mo^{-1}).

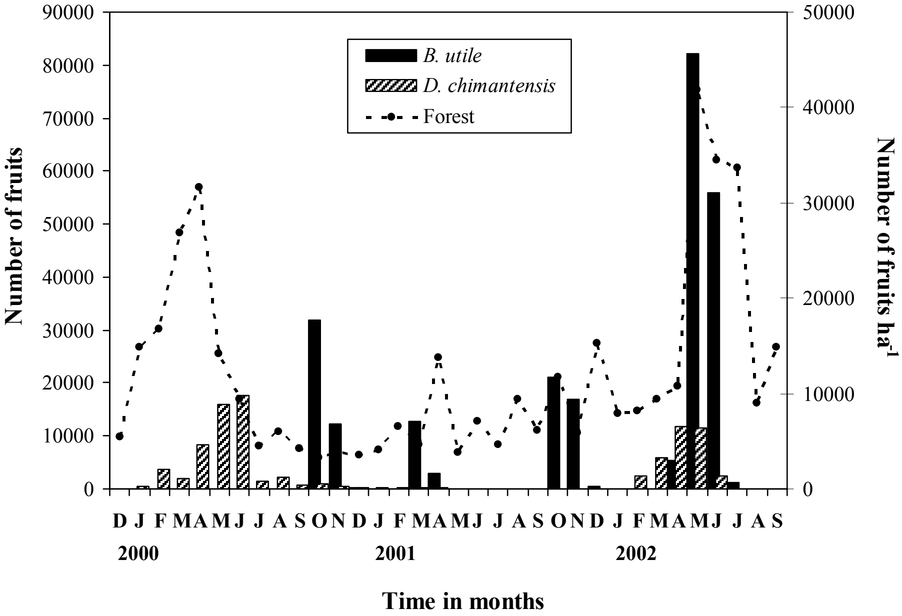

Figure 5.1. Monthly fruiting patterns of *Dacryodes chimantensis* (n = 16) and *Brosimum utile* (n = 10) in a terra firme rain forest, Colombian Amazonia. Community wide fruiting pattern (December 1999–September 2002; see Chapter 3) is represented by the dashed line.

5.5.2 Seed Dispersal

Percentage of seeds removed per tree by diurnal frugivores, relative to the total fruit crop size, was similar in both species (*Dacryodes* 1.8 ± 0.6%; *Brosimum* 2.0 ± 1.9%). However, frugivores removed more seeds of *Brosimum* than *Dacryodes*, both in absolute numbers (1388 seeds and 61 seeds, respectively), and per observation hour (3.1 seeds h^{-1} and 0.1 seeds h^{-1}, respectively).

Six bird-species were observed visiting *Dacryodes* trees, but just three were frugivores (Table 5.2). Only the parrots *Amazona festiva* and *A. amazonica* removed seeds, but destroyed and/or dropped under the tree crown all fruits removed. A total of six species of birds and two species of primates were observed feeding on the fruits of *Brosimum* (Table 5.2). The primate species *Saguinus fuscicollis* was the most important disperser of *Brosimum* seeds. It exhibited the highest number of visits (29), removed and dispersed the highest number of seeds (974 and 586, respectively). Among birds, *Pteroglossus pluricinctus* was by far the most regular visitor and the major disperser of *Brosimum* (Table 5.2). Although the number of seeds removed by toucans (Ramphastidae) was lower than *S. fuscicollis,* they were more effective dispersers, since most of the seeds removed were carried away from the parent tree (Table 5.2).

Although mammals were never observed feeding at *Dacryodes* trees, 64.7% of the 480 seeds deposited by animals between 0 and 50 m from the base of the parent tree, were clearly handled by mammals (arboreal and ground), and 35.3% by birds (Figure 5.2). *Dacryodes* seeds handled by birds were deposited at a mean of 6.9 m away from the parent tree (Confidence 95% limits = 5.1–8.6 m), and seeds handled by mammals at 6.6 m (Cl = 4.9–8.3 m). Distribution of both bird and mammal-handled seeds was highly leptokurtic and skewed towards the parent tree (birds: skewness = 5.05; SE = 0.36; kurtosis = 28.92, SE = 0.71; mammals: skewness = 6.05; SE = 0.33; kurtosis = 39.91, SE = 0.66; Figure 5.3). Of the 682 *Brosimum* seeds deposited by vertebrates on the ground, 78.7% were handled by arboreal and ground mammals, while 21.3% by birds. *Brosimum* seeds handled by birds were deposited at a mean of 11.5 m away from the parent tree (Cl = 8.9–14.0 m), while seeds handled by mammals at 16.1 m (Cl = 14.1–18.2 m). Seeds were closer to the parent tree than expected from the statistically normal distribution (Birds: skewness = 1.50; SE = 0.36; Mammals: skewness = 1.21; SE = 0.18; Figure 5.3). The distribution of seeds handled by mammals was not leptokurtic (kurtosis = 0.42, SE = 0.35), while the distribution of bird-handled seeds was weakly leptokurtic (kurtosis = 1.93, SE = 0.70).

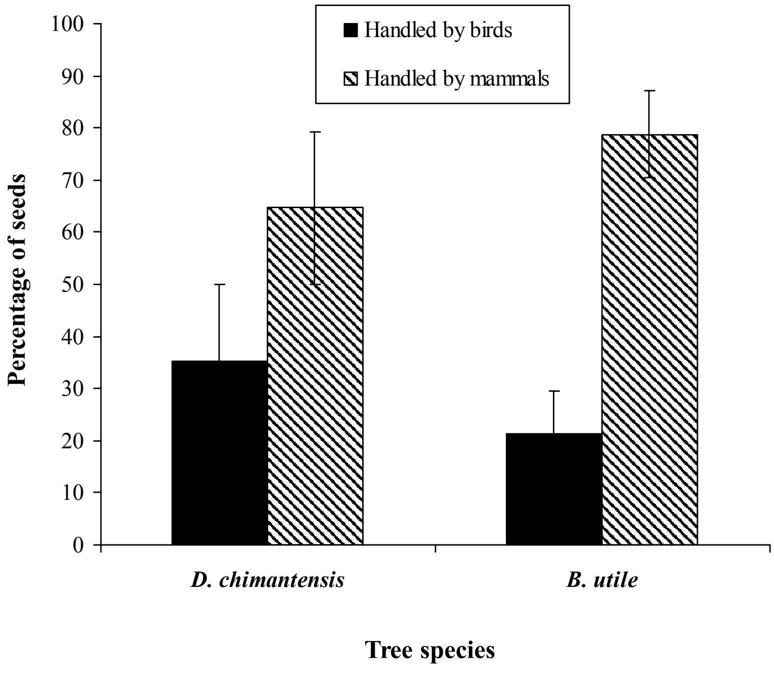

Figure 5.2. Mean percentage of seeds deposited on the ground by frugivores per parent tree (n = 5) of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia

Table 5.2. Diurnal frugivores recorded at the canopy level of *Dacryodes chimantensis* and *Brosimum utile* trees in a terra firme rain forest, Colombian Amazonia. N: sample sizes (number of visits), removal success (number of seeds removed), dispersal success (seeds carried away, and percentage of seeds taken away relative to the seeds removed) for each vertebrate species visiting the tree (*D. chimantensis* 202 observation h; *B. utile* 90 observation h). Scientific names and order of species follows Emmons and Feer (1990) and Hilty and Brown (1986).

Frugivore species		Removal success		Dispersal success	
Family	Species and common names	N	(No. seeds)	(No. seeds)	%
Dacryodes chimantensis					
Psittacidae	**Amazona festiva* (Festive parrot)	8	26	0	0
	**Amazona amazonica* (Orange-winged parrot)	6	35	0	0
Ramphastidae	*Ramphastos cuvieri* (Cuvier's toucan)	1	0	0	0
Picidae	*Celeus elegans* (Chestnut woodpecker)	1	0	0	0
Thamnophilidae	*Myrmotherula* cf. *multiostrata* (Amazonian streaked-antwren)	1	0	0	0
Coerebidae	*Cyanerpes caeruleus* (Purple honey creeper)	2	0	0	0
	Total	**19**	**61**	**0**	**0**
Brosimum utile					
Psittacidae	* *Amazona farinosa* (Mealy parrot)	7	42	6	14.3
	* *Amazona sp.*	6	58	11	19.0
Ramphastidae	*Pteroglossus pluricinctus* (Many-banded aracari)	11	145	138	95.2
	Ramphastos tucanus (White-throated toucan)	7	54	48	88.9
	Selenidera reinwardtii (Golden-collared toucanet)	6	31	29	93.5
Cotingidae	*Tityra inquisitor* (Black-crowned tityra)	6	33	21	63.6
Callithrichidae	*Saguinus fuscicollis* (Saddle-back tamarin)	29	974	586	60.2
Cebidae	*Callicebus torquatus* (Collared titi)	16	51	33	64.7
	Total	**88**	**1388**	**872**	**62.2 %**

* Seed predators (*sensu* Snow 1981)

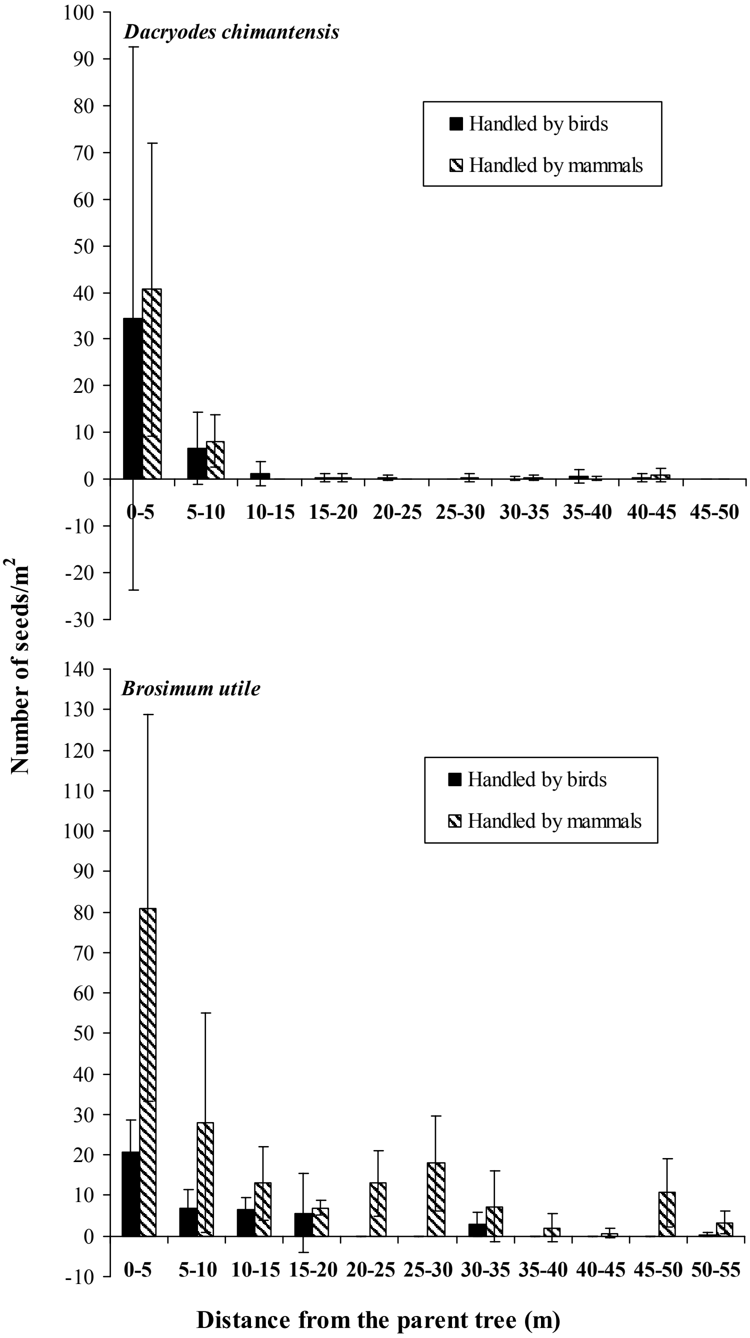

Figure 5.3. Seed deposition by frugivores at different distances from the parent tree of *Dacryodes chimantensis* (a) and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia. Distance class 0-5 m is below the crown of *Dacryodes* trees . Distance classes 0 –5 and 5 –10 are below the crown of *Brosimum* trees.

5.5.3 Seed shadow

Natural distribution of seeds between 0-50 m from the base of the parent plant was more leptokurtic and skewed towards the parent tree in *Dacryodes* than in *Brosimum* (Table 5.3; Figures 5.4, 5.5). The mean dispersal distance of *Dacryodes* seeds was 7.1 m, while 12 m for *Brosimum.*

Total predation of *Dacryodes* seeds found between 0-50 m from the parent tree was 45.1 ± 17.8%. Major causes of seed mortality were fungi and larvae, while vertebrates (mainly parrots) were less important (Figure 5.6). The total percentage of predated seeds of *Brosimum* was lower (26.4 ± 12.8%) than *Dacryodes.* Bruchid beetle larvae was the major cause of death of *Brosimum* seeds, while predation by vertebrates was insignificant (Figure 5.6). Fungal damage was not observed in any *Brosimum* seed. Predation of *Brosimum* seeds was highly clumped near the parent tree (Table 5.3), while predation of *Dacryodes* seeds was spread over the 50 m radius from the base of the parent plant.

Total seed predation of *Dacryodes* and *Brosimum,* and seed predation by invertebrates were positively correlated with seed density, and negatively correlated with the distance to the parent tree (Table 5.4). Seed predation by vertebrates was not correlated with distance and density in *Brosimum*. Seed predation by fungi was only observed in *Dacryodes*, and was both distance and density-dependent.

Table 5.3. Summary of the shape of the seed shadow per parent tree of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia. Cl: Confidence 95 % limits; SE: standard error. Bold type: normal distribution.

Tree species	Mean (m)	Cl (m)	Skewness	SE	Ratio Skewness/SE	Kurtosis	SE	Ratio Kurtosis/SE
Viable seeds								
D. chimantensis	7.1	6.2-8.0	4.23	0.19	22.27	21.07	0.38	55.75
B. utile	12.0	11.0-12.9	1.91	0.10	18.67	2.85	0.20	13.97
Predated seeds								
D. chimantensis	5.8	5.5-6.0	1.97	0.20	9.99	1.89	0.39	4.83
B. utile	8.9	7.8-10.0	3.03	0.16	18.53	9.53	0.33	29.31

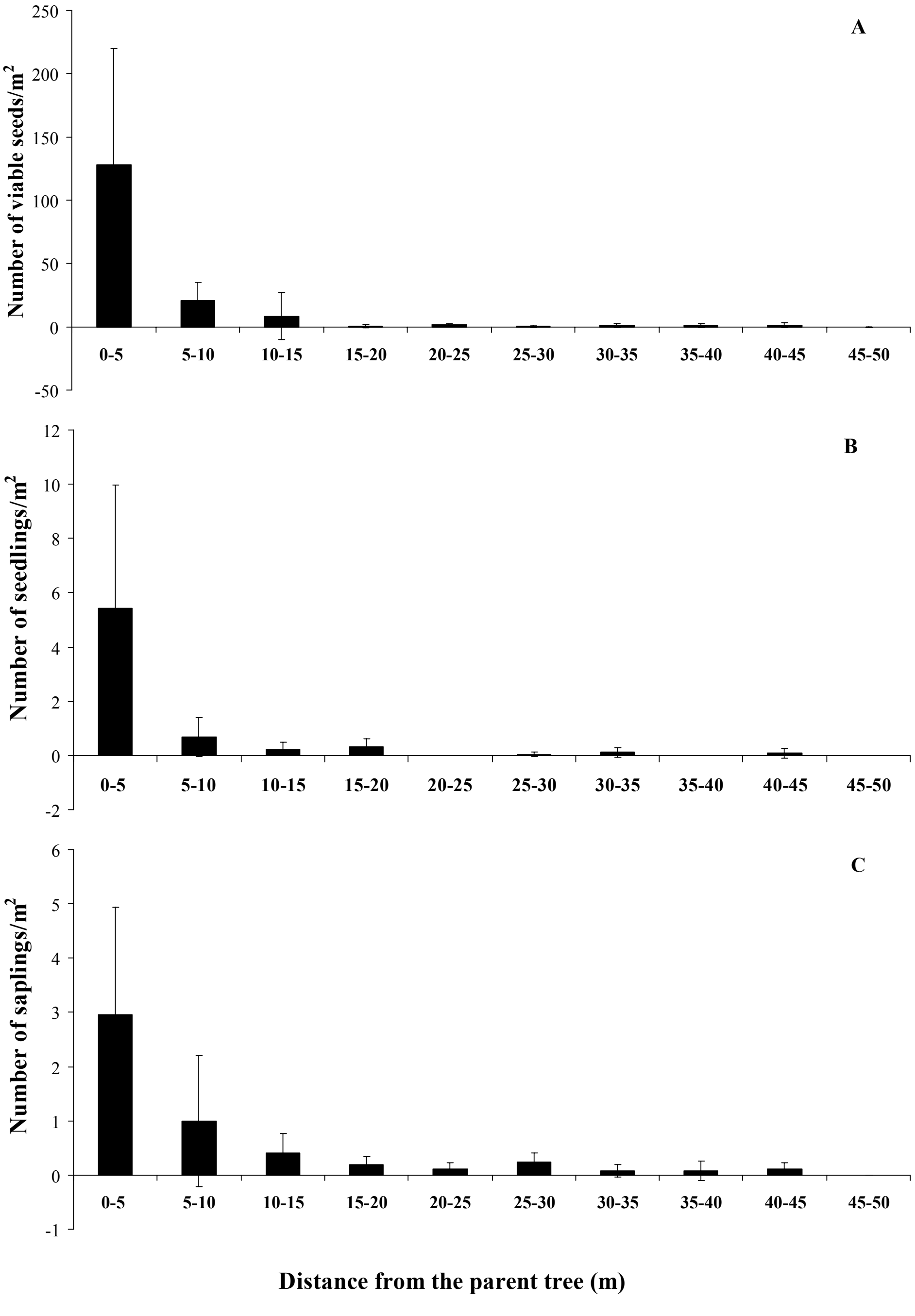

Figure 5.4. Seed (a), seedling (b) and sapling (c) shadow per parent tree of *Dacryodes chimantensis* in a terra firme rain forest, Colombian Amazonia.

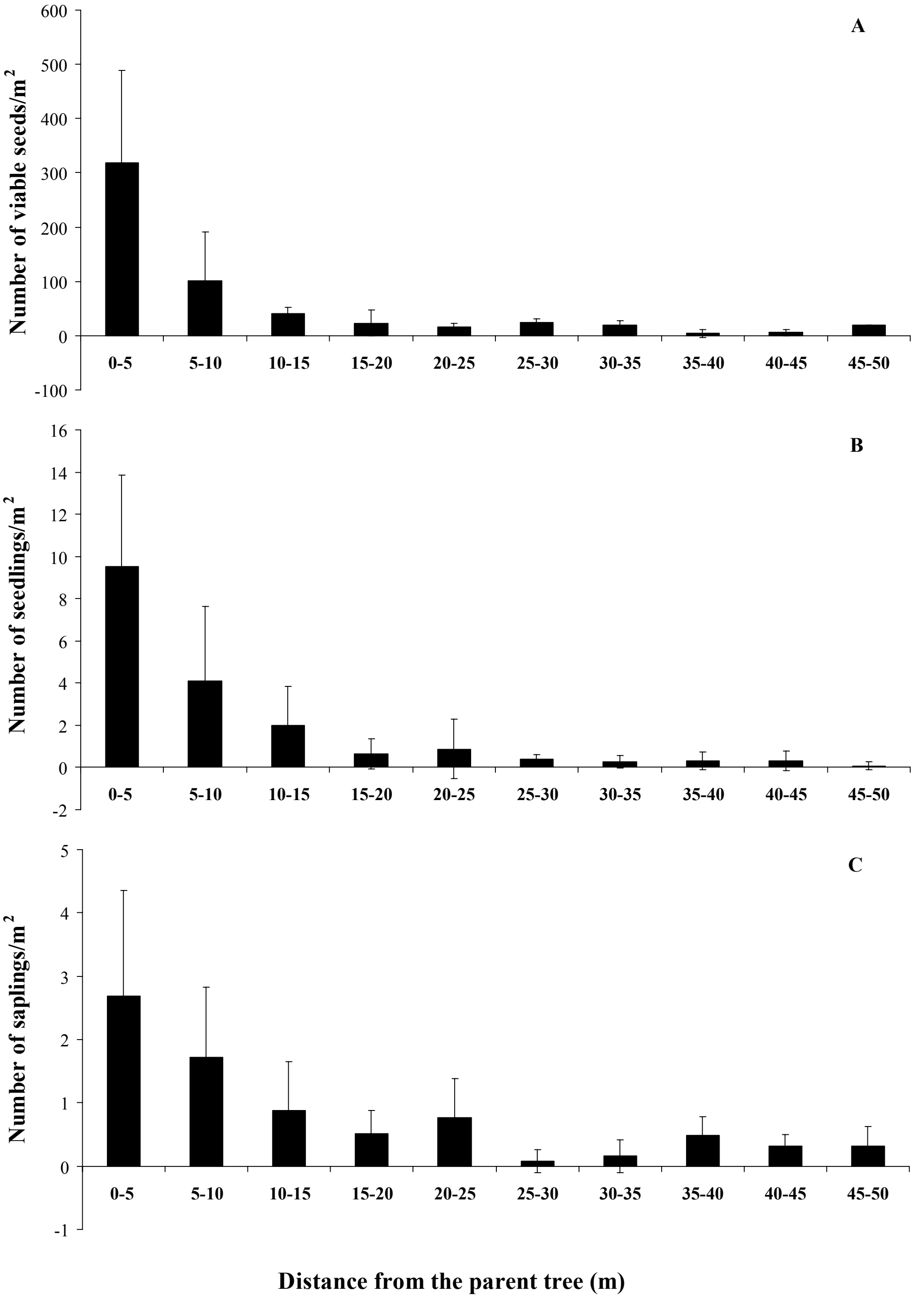

Figure 5.5. Seed (a), seedling (b) and sapling (c) shadow per parent tree of *Brosimum utile* in a terra firme rain forest, Colombian Amazonia.

Table 5.4. Effect of distance from the parent tree and seed density on seed predation of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia. r_s: Spearman rank correlation. Bold type: $P < 0.005$, $N = 50$.

	Dacryodes chimantensis		*Brosimum utile*	
	r_s	P	r_s	P
Total seeds predated				
vs. distance	**-0.680**	<< 0.001	**-0.384**	**0.028**
vs. density	**0.833**	<< 0.001	**0.677**	<< 0.001
Seeds predated by invertebrates				
vs. distance	**-0.644**	<< 0.001	**-0.590**	<< 0.001
vs. density	**0.800**	<< 0.001	**0.785**	<< 0.001
Seeds predated by fungi				
vs. distance	**-0.656**	<< 0.001	-	-
vs. density	**0.701**	<< 0.001	-	-
Seeds predated by vertebrates				
vs. distance	**-0.483**	<< 0.001	-0.074	0.680
vs. density	**0.537**	<< 0.001	-0.263	0.139

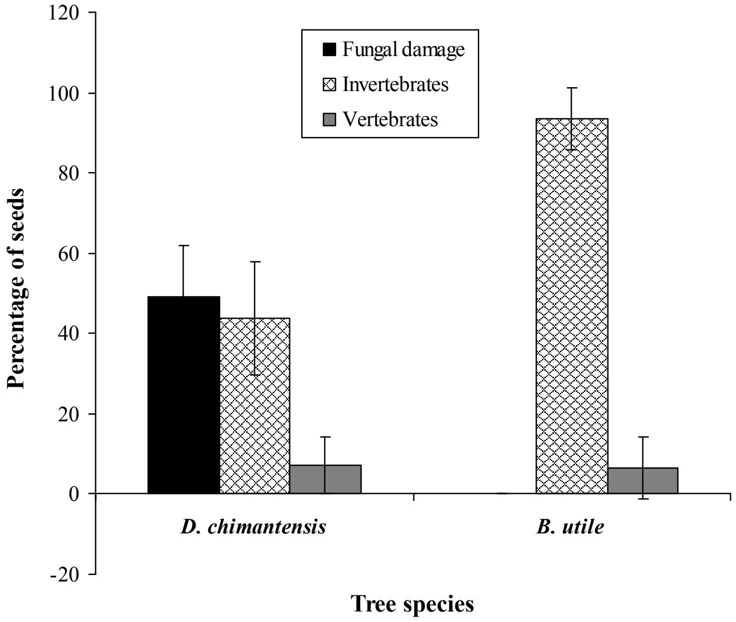

Figure 5.6. Seed predation and causes of seed death per parent tree of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia.

5.5.4 Seeding and sapling shadow

The seedling shadow of *Dacryodes* was more leptokurtic and skewed towards the parent tree in *Dacryodes* than in *Brosimum* (Table 5.5; Figures 5.4, 5.5). Distribution of *Dacryodes* saplings was flatter and less skewed towards the parent tree than its seedlings. Distribution of *Brosimum* saplings was non-leptokurtic (Table 5.5; Figures 5.4, 5.5).

Damage or potential predation of *Dacryodes* seedlings between 0-50 m was 30.1 ± 12.9%, while damage of *Brosimum* seedlings was 19.4 ± 10.8%. At the sapling stage, total damage of *Dacryodes* saplings was 43.9 ± 10.8%, and 31.9 ± 13.2% in *Brosimum*. Causes of damage of seedlings and saplings of both species were disease and herbivores (Figure 5.7). At the seedling stage, herbivores were the major cause of damage of *Dacryodes* seedlings, while disease was more important in *Brosimum* (Figure 5.7a). Herbivores were the major cause of damage in the sapling stage of both species (Figure 5.7b). For both species damage of seedling and sapling was weakly or non-leptokurtic (Table 5.5).

Table 5.5. Summary of the shape of the seedling and sapling shadow per parent tree of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia. Cl: Confidence 95 % limits. SE: standard error. Bold type: normal distribution.

Tree species	Mean (m)	Cl (m)	Skewness	SE	Ratio Skewness/SE	Kurtosis	SE	Ratio Kurtosis/SE
Viable seedlings								
D. chimantensis	7.5	5.3-9.7	3.18	0.40	7.88	11.07	0.79	14.05
B. utile	11.0	9.1-13.0	2.06	0.25	8.19	3.93	0.50	7.90
Damaged seedlings								
D. chimantensis	7.2	3.3-11.1	2.51	0.72	3.49	6.34	1.40	4.53
B. utile	9.7	6.4-12.9	1.40	0.58	2.42	2.10	1.12	**1.87**
Viable saplings								
D. chimantensis	10.6	6.6-14.5	2.33	0.46	5.12	5.76	0.89	6.50
B. utile	17.0	12.5-21.5	1.18	0.37	3.16	0.23	0.73	**0.31**
Damaged saplings								
D. chimantensis	8.6	5.2-12.0	1.37	0.66	2.08	1.32	1.28	**1.03**
B. utile	12.3	4.9-19.7	1.95	0.66	2.95	3.63	1.28	2.84

Overall damage, damage by herbivores, and damage from disease of *Dacryodes* seedlings and saplings, were positively correlated with density, and negatively correlated with distance from the parent tree (Table 5.6). *Brosimum* seedling damage and its causes were also correlated with seedling density and distance. Total sapling damage and damage from disease were only correlated with distance from the parent tree (Table 5.6).

Table 5.6. Effect of natural distance from the parent tree and density on damage experienced by seedlings and saplings of *Dacryodes chimantensis* and *Brosimum utile* and causes of damage in a terra firme rain forest, Colombian Amazonia. Bold type: $P < 0.05$, $N = 50$.

	Dacryodes chimantensis				*Brosimum utile*			
	Seedlings		Saplings		Seedlings		Saplings	
	r	P	r	P	r	P	r	P
Total damage								
vs. distance	**-0.501**	<< 0.001	**-0.449**	0.001	**-0.716**	<< 0.001	-0.225	0.117
vs. density	**0.665**	<< 0.001	**0.625**	<< 0.001	**0.654**	<< 0.001	**0.299**	0.035
Damage from herbivores								
vs. distance	**-0.477**	<< 0.001	**-0.441**	0.001	**-0.596**	<< 0.001	-0.276	0.052
vs. density	**0.628**	<< 0.001	**0.620**	<< 0.001	**0.507**	<< 0.001	0.272	0.056
Damage from disease								
vs. distance	**-0.381**	0.006	**-0.487**	<< 0.001	**-0.632**	<< 0.001	-0.263	0.065
vs. density	**0.393**	0.002	**0.572**	<< 0.001	**0.716**	<< 0.001	**0.455**	<< 0.001

5.5.5 Seedling establishment and recruitment

For each distance class, the probability of transition of *Dacryodes* seeds to the seedling stage was lower than 0.1 (Figure 5.8). The highest probability of transition from the seed to the seedling stage was recorded between 0-5 m distance from the parent tree, followed by the 5-10 m and 30-35 m distance classes (Figure 5.8). For *Brosimum,* the highest probability of transition from seed to seedlings (0.12) occurred at 20-25 m from the parent tree, and the second at 10-15 m (Figure 5.9).

The highest probabilities of transition from the seedling to the sapling stage of *Dacryodes* were between 0-20 m distance from the parent tree, with the highest occurring in the 5-10 m distance class (Figure 5.8). For *Brosimum* the highest probability of transition from seedlings to saplings occurred at 15-20 m from the parent tree (Figure 5.9).

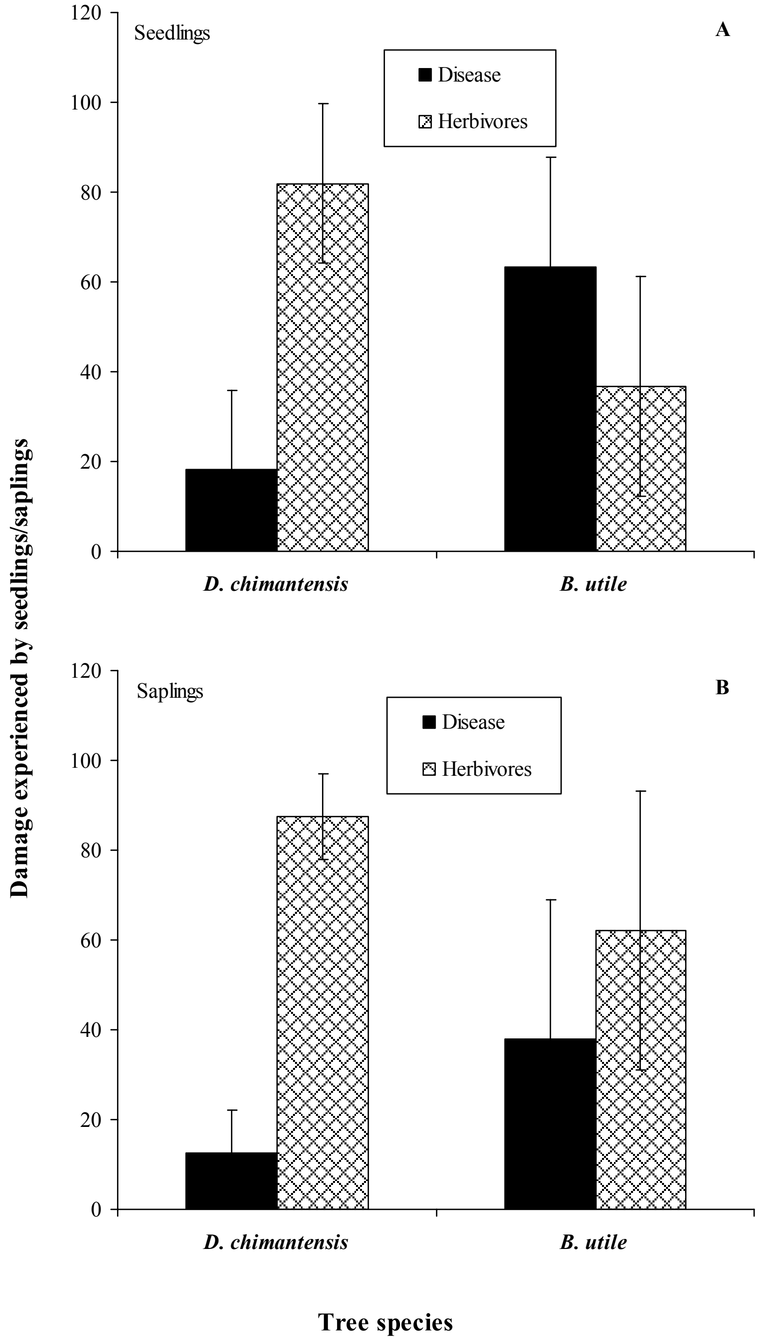

Figure 5.7. Potential damage and causes of damage per parent tree experienced by seedlings (a) and saplings (b) of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia.

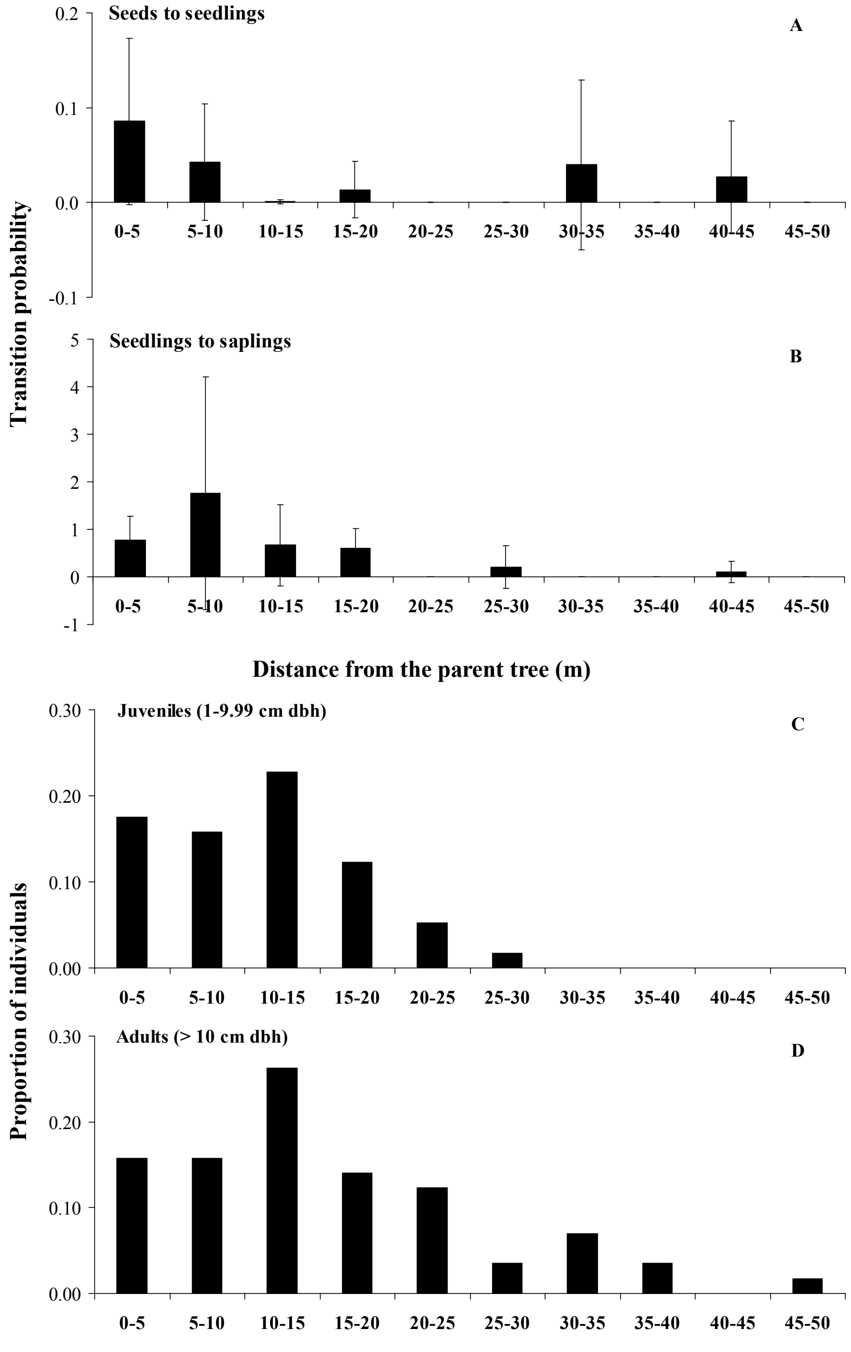

Figure 5.8. Probability of transition of seeds to the seedling stage (a), and of seedlings to the sapling stage (b); and relative proportions of distances to the first nearest neighbours for juveniles (c), and adults (d) of *Dacryodes chimantensis* in a terra firme rain forest, Colombian Amazonia.

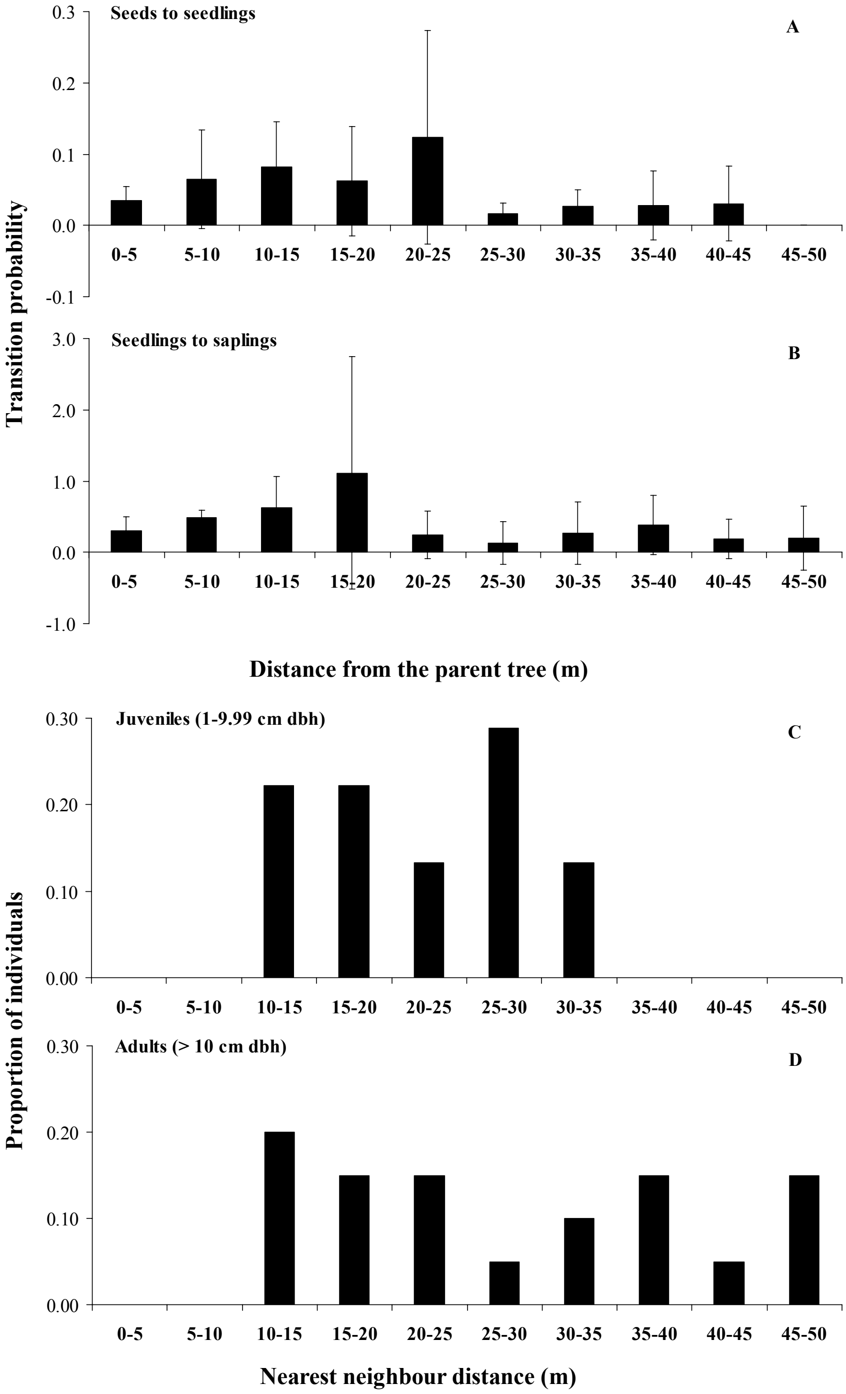

Figure 5.9. Probability of transition of seeds to the seedling stage (a), and of seedlings to the sapling stage (b); relative proportions of distances to the first nearest neighbours for juveniles (c), and adults (d) of *Brosimum utile* in a terra firme rain forest, Colombian Amazonia.

5.5.6 Distribution and densities of juvenile and adults

In the study area, density of adult *Dacryodes* trees (≥ 10 cm dbh) estimated for the plot-based censuses was 5.9 trees ha^{-1} (Cl = 5.7–6.2 trees ha^{-1}), while *Dacryodes* juveniles (1-9.99 cm dbh) density was 10.1 juveniles ha^{-1} (Cl = 9.7–10.6 juveniles ha^{-1}). Density estimates for *Brosimum* derived from the plot-based census was 3.5 trees ha^{-1} (Cl = 2.6–5.3 trees ha^{-1}), and 3.2 juveniles ha^{-1} (Cl = 2.3–5.6 juveniles ha^{-1}). For the transect-based estimates, density of *Brosimum* was 6.6 adult trees ha^{-1} (Cl = 4.5–9.8 trees ha^{-1}), and 8.1 juveniles ha^{-1} (Cl = 5.7–11.5 juveniles ha^{-1}).

Mean observed nearest neighbour distance for *Dacryodes* juveniles (10.9 ± 6.0 m) was lower than the nearest neighbour distance expected (21.3 m), indicating tendency towards clumping (Table 5.7). Nearest neighbours were skewed towards short distances, with more than 50% of all juveniles being within 15 m of each other (Figure 5.8c). A clumped pattern was observed for *Dacryodes* adults (Table 5.7), but few individuals were found beyond 20 m away from each other (Figure 5.8d). As indicated by the standard deviation, distances to the nearest neighbours were not significantly different between adults and juveniles. The Donnelly index of aggregation and the Hopkins' test indicated that both *Dacryodes* adults and juveniles were clumped in the study area (Hopkins' test = trees $F_{0.975,\ 114,114} = 1.43$, $P > 0.05$; juveniles $F_{0.975,\ 88,88} = 1.55$, $P > 0.05$).

Table 5.7. Mean observed distances to the nearest neighbour, Donnelly index of aggregation (Donelly 1978) and the Hopkins' test statistic for randomness (Hopkins 1954) obtained for juvenile (1-9.99 cm dbh) and adult (≥ 10 cm dbh) trees of *Dacryodes chimantensis* and *Brosimum utile* in a terra firme rain forest, Colombian Amazonia.

	Distance to the nearest neighbour (m)			Spatial distribution					
		Observed		Donnelly index of aggregation			Hopkins' test for randomness (h)		
Tree species	Expected	Mean	SD	R	z	Pattern	h	d.f (2n)	Pattern
D. chimantensis									
Adult	18.3	15.4	9.9	0.84	-1.99	aggregated	2.60	114	aggregated
Juveniles	21.3	10.9	6	0.51	-5.30	aggregated	4.15	88	aggregated
B. utile									
Adult	22.7	25.2	13.7	1.11	0.50	random	1.32	14	random
Juveniles	24.9	20.2	7.5	0.81	-0.76	random	4.73	12	aggregated

Regarding *Brosimum*, although mean observed nearest neighbour distance of juveniles (20.2 ± 7.5 m) was lower than expected, the Donnelly index and the

Hopkins' test showed contrasting distribution patterns (Table 5.7). While the first index indicated that *Brosimum* juveniles exhibit a random distribution pattern, the second indicates that the pattern is clumped ($F_{0.975,\ 12,12} = 3.28$, $P > 0.05$; Table 5.7). For *Brosimum* trees $\geq$ 10 cm dbh, mean observed nearest neighbour distance was higher than expected, indicating no tendency towards clumping (Table 5.7). The null hypothesis of randomness was accepted for *Brosimum* adults as $h = 1.32$ was within the F-values range ($F_{0.025,\ 14,14} = 0.34$, $F_{0.975,\ 14,14} = 2.98$, $P < 0.05$). The Donnelly index also indicated a random distribution pattern of *Brosimum* adults (Table 5.7). The transect-based census showed a non-clustered distribution pattern of both juveniles and adults of *Brosimum*, since 21 (53%) of the 100-m transect segments censused ($n = 40$) contained 100 % of adults detected, and 18 (48%) of juveniles. Distances to the nearest neighbour did not show significant differences between adults and juveniles. All *Brosimum* juveniles (100%) were concentrated between 10-35 m from each other (Figure 5.9c), while no adult trees were found at less than 10-m distance from each other (Figure 5.9d).

The spatial patterns of seed, seedling, sapling, juvenile and adult stages of *Dacryodes* were consistent with each other (Table 5.8). Also, the spatial patterns of *Brosimum* seeds, seedlings and saplings were significantly related, but not the sapling and juvenile stages, nor between juveniles and adults.

Table 5.8. Correlation matrix between spatial distribution of *Dacryodes chimantensis* and *Brosimum utile* at different life stages in a terra firme rain forest, Colombian Amazonia. Damaged seedlings and saplings are not included in the calculations. Spearman Rank correlation (r_s), Bold type: $P < 0.05$, $N = 10$.

Life stage			Seedling	Sapling	Juvenile	Adult
D. chimantensis						
	Seed	r_s	0.747	0.671	0.657	0.683
		P	**0.013**	**0.034**	**0.039**	**0.030**
	Seedling	r_s		0.675	0.696	0.751
		P		**0.032**	**0.025**	**0.012**
	Sapling	r_s			0.777	0.592
		P			**0.008**	0.071
	Juvenile	r_s				0.922
		P				**0.000**
B. utile						
	Seeds	r_s	0.717	0.564	0.215	-0.409
		P	**0.020**	**0.090**	0.551	0.240
	Seedlings	r_s		0.802	0.078	-0.290
		P		**0.005**	0.830	0.416
	Saplings	r_s			-0.286	-0.063
		P			0.422	0.863
	Juveniles	r_s				0.365
		P				0.300

5.6 DISCUSSION

Results of the present study support the hypothesis that on the local scale, the spatial distribution patterns of *Dacryodes* and *Brosimum,* are largely driven by the combined effect of the dispersal agent and the seed displacement. This concurs with other studies suggesting that differential seed dispersal by animals is the most likely explanation for the observed spatial patterns of some tree populations in tropical forests (Bleher and Böhning-Gaese 2001, Fragoso 1997, Silva-Matos and Watkinson 1998). In this study, the low number of frugivores visiting *Dacryodes* trees, the shorter seed dispersal distances, and the clumped deposition of *Dacryodes* seeds near the parent tree seem to explain the clumped distribution patterns of adults across the study site. This contrasts with the more scattered (random) spatial pattern of *Brosimum* adult trees related to the more efficient dispersal of *Brosimum* seeds by frugivores, the longer seed dispersal distances and less leptokurtic seed shadows. It seems hence, that abiotic factors such as climate, light levels, gap size and so forth, are likely to equally affect the growth of both species (Clark *et al.* 1999, Bleher and Böhning-Gaese 2001, Hamill and Wright 1986).

5.6.1 Frugivory and dispersal agents

Frugivory and seed dispersal was higher and more efficient in *Brosimum* than in *Dacryodes* in terms of the number of dispersal agents, the quantity and quality of their feeding behaviours, and the number of seeds transported away from the parent tree. The saddle-back tamarin (*Saguinus fuscicollis*) and the many-banded aracari (*Pteroglossus pluricinctus*) were the main diurnal mammal and bird dispersers of *Brosimum* seeds. Both species performed high quantity and quality behaviours (*sensu* Jordano and Schupp 2000) such as visiting the trees on a regular basis, high percentages of seed dispersed, and short visits which diminish the probability of regurgitating or defecating seeds beneath the parent plant. Observations of toucans (*P. pluricinctus, R. tucanus, S. reinwardtii*) are consistent with previous studies suggesting these birds as leading seed dispersers in tropical rain forests (Galleti *et al.* 2000, Howe 1993, Snow 1981). As with other studies (Jansen and Zuidema 2001, Janzen 1991), ground mammals were important dispersers of *Brosimum* seeds. Marks on handled fruits and seeds found on the ground, indicated that both tamarins and rodents were dispersing significant amount of *Brosimum* seeds. Although some studies have found that the removal of small seeds by rodents (< 1 g, < 1 cm) mostly accounts for predation (Forget *et al.* 1998), we found that overall seed predation by vertebrates was insignificant.

Observed movement patterns and feeding behaviours of tamarins and rodents feeding on *Brosimum* seeds indicate that they can be depositing *Brosimum* seeds at medium distances from the parent tree (15-30 m), mainly in the 10-15 m and 25-30 m distance classes. For instance, a tamarin troop moved between 18.7 and 27.6 m after a feeding bout from their original fruiting tree until the next stop (*e.g.* fruiting tree), where they often deposited an important number of seeds (A. Parrado-Rosselli unpublished data). In addition, observed movement patterns and feeding behaviours of toucans indicate that they can deposit *Brosimum* seeds between 10-15 m away from the parent plant (A. Parrado-Rosselli unpublished data).

In contrast to the seed dispersal observed in *Brosimum*, no particular species or set of frugivores were found to be dispersing *Dacryodes* seeds. Only parrots were observed to feed on *Dacryodes* fruits, but their feeding behaviours resulted in predation and deposition of seeds beneath the parent tree. Examination of handled fruits found on the ground, indicated that mammals also consumed fruits of *Dacryodes*, but they did not deliver seeds further than 10 m from the parent tree. This low and inefficient seed dispersal by animals (in the few cases were it occurred) of *Dacryodes* seeds, resulted in very few seeds landing (mainly by birds action) a few meters away from the parent tree, particularly, within the 10-15 m distance class.

Plant characteristics also impose limitations on seed dispersal (Muller-Landau *et al.* 2002). Fruit and seed size, fruit crop sizes and fruiting patterns are major factors determining the food selection of all consumer species (Altrichter *et al.* 2002, Di Fiore 2003, Forget *et al.* 2002, Galetti and Aleixo 1998, Henry 1999, Parrado-Rosselli *et al.* 2002, Peres 1994, Silvius and Fragoso 2003, Stevenson *et al.* 2000, Wenny 2000b). In this study, the smaller fruit and seed size of *Brosimum* may have resulted in a greater number of seeds being dispersed by frugivores (Parrado-Rosselli *et al.* 2002). Additionally, although *Brosimum* fruited more frequently than *Dacryodes*, major fruit production peaks of both species occurred during the peak of fruit abundance in the forest, a time when many frugivores feed on more preferred fruits with larger crops, than when fruits are scarce (Howe and Estabrook 1977, Nathan and Muller-Landau 2000, Snow 1971). It appears that frugivores are preferring *Brosimum* to *Dacryodes* fruits, which are offered in significantly larger fruit crop sizes.

5.6.2 From seeds to subsequent life stages

For both *Dacryodes* and *Brosimum* there was consistency between their seed shadows and the spatial distribution of subsequent life stages. Although seed density of both species declined leptokurtically with distance, and was skewed towards the parent tree, seed density was more skewed and leptokurtic in *Dacryodes* than in *Brosimum.* Distributions of the saplings of both species tended to be flatter and more distant from the parent tree, but the overall trend of *Dacryodes* for peaking nearer the parent tree than *Brosimum* was maintained in the seedling and in the sapling stage. Additionally, in agreement with the clumped deposition pattern of *Dacryodes* seeds, the spatial distribution pattern of both juvenile and adults was found to be aggregated. Mean observed distances to the nearest neighbour of *Dacryodes* juveniles (10.9 m) and adults (15.4 m), were consistent with the 10-15 m distance class, where 6% of the seeds were deposited mainly by birds, with the highest probability of transition from seeds to seedlings and saplings, and with the highest concentration of first neighbours for both juvenile and adult stage. For *Brosimum,* the random pattern exhibited by adults indicated a low deviation from the more scattered pattern of seed deposition and from the highest probabilities of transition from seeds to seedlings and saplings. Mean observed distances to nearest neighbours corresponded well (albeit not exactly) with distances where many seeds were found, and with post-feeding movements of the main seed dispersers of *Brosimum.*

However, the spatial pattern of *Brosimum* juveniles was partially related to the pattern observed for seeds, seedlings, saplings and adults. This may be a consequence of the different methodologies used in this study being sensitive to differences in local abundance (*i.e.* plot vs. transect-based censuses), and due to other factors not considered when assuming that juveniles and adults originate from the same seedlings sampled. Nevertheless, the high densities of juveniles may also be due to toxic phyto-chemicals in leaves of *Brosimum* juvenile, which protect the plant from predation as with other Moraceae species (Sgarbieri *et al.* 1964). The species is, therefore, able to spend a long time in the immature-juvenile stage.

5.6.3 Predation and survival

The role of seed dispersal in shaping the *future* distribution of seedling and saplings also depends on the seed and seedling predation patterns (Clark *et al.* 1999, Bleher and Böhning-Gaese 2001, Schupp 1990). Even though overall seed predation was higher in *Dacryodes* than in *Brosimum* (45% and 26%, respectively), percentages of predated seeds of both species were lower than seed predation percentages of many other tropical plant species (range = 75 to 99%; Brewer and Webb 2002, Fragoso 1997, Howe 1982, Kiltie 1981, Silva-Matos and Watkinson 1999, Smythe 1989). Seed predation and seedling damage (potential predation) of both species was highly distance and density-dependent (Janzen 1970, Connell 1971), but stronger in *Brosimum*. Thus, the successful recruitment of *Brosimum* is increased when its seeds are transported at greater distances from the parent tree. *Dacryodes*, in contrast compensates for the effect of being less preferred by animals by maintaining a higher survivorship capacity close to the parent tree (*ca.* 10–15 m), by having extended fruiting seasons, and by offering fewer ripe fruits over long time periods. These characteristics have been suggested as strategies for avoiding competition for seed dispersers and minimising seed predation (Foster 1982, Smythe 1970, Wright *et al.* 2005).

As with other studies, predation by vertebrates was of minor importance compared with predation by invertebrates and pathogens (Forget 1990, Hammond and Brown 1998, Hammond *et al.* 1999). Predation by vertebrates was not distance nor density dependent, suggesting that vertebrates forage throughout their home ranges, without being influenced by the gradient of declining seed density with distance from the parent tree (Hammond and Brown 1998, Hammond *et al.* 1999). The effect of terrestrial vertebrates on predation is probably stronger in species with larger and heavier seeds, generally preferred by this kind of animals (Jansen *et al.* 2004). Comparisons of a broader range of fruit/seed-sized tree species, may demonstrate whether commonness and regularity in fruit production are the only plant characteristics to be considered when predicting the effect of animal seed dispersal on the spatial patterns of trees in a mixed-species plant community.

5.6.4 Final considerations

The observed patterns of deposition and dispersal of the seeds of both tree species studied here, does not necessarily imply that some seeds can not be transported by animals at greater distance from the parent trees. For instance, during casual observations, the bird species *Penelope jacquacu* and *Ramphastos cuvieri* were recorded feeding on *Dacryodes* fruits. Also, the lipid-rich *Dacryodes* fruits are important components of the diet of oilbirds (*Steatornis caripensis;* Snow 1962). Thus, the occasional seed dispersal events by mammals, toucans, and/or oilbirds may result in a few seeds delivered in longer distances away from the parent tree, and are sufficient to explain the creation of a new patch. In addition, the high ratio of *Dacryodes* seedlings established between 30-35 m distance from parent trees, and the presence of some adults in this distance class, may be the consequence of a few seeds deposited by animals during previous reproductive seasons. In the case of *Brosimum* terrestrial mammals, but also terrestrial birds (*e.g.* Grey-winged Trumpeter - *Psophia crepitans*; A. Parrado-Rosselli unpublished data) may also be dispersing few seeds over greater distances, as occurs in other rodent-dispersed seed species (Forget 1996, Jansen *et al.* 2004, Peres and Baider 1997). This may result in a more scattered pattern, and an increased spacing between conspecifics.

Previous hypthesis about the possible effects of seed dispersal on patterns of spatial distribution have been mainly focused on seed dispersal modes (*i.e.* wind, birds, mammals), suggesting for example, that mammal-dispersed plant species are more clumped than bird or wind-dispersed species (Hamill and Wright 1986, Hubbell 1979). When considering *Dacryodes* as a bird-dispersed species and *Brosimum* as a mammal-dispersed species, their dispersal modes would not have adequately predicted the possible consequences of seed dispersal on the recruitment patterns of these tree species. Our results demonstrate that the combined effect of quantity and quality behaviours of frugivores and the seed displacement by all dispersal agents is more important when predicting the spatial patterns of common tree species in the terra firme rain forests of Colombian Amazonia.

The spatial pattern of common tree species may also provide insights into their seed dispersal processes and main dispersal agents. Long-term studies with a larger set of tree species with similar features (commonness, fruiting synchrony and periodicity) would provide more evidence for predicting the effect of seed dispersal by animals. This may have important implications in conservation planning and reserve design, as it will provide tools for managing both species vulnerability following habitat alteration, and species composition without altering the dynamics and carrying capacity of the forest (Howe 1990, Terborgh 1990).

Given that patterns of seed dispersal, seed fall, and seedling establishment were obtained for a single fruiting season (single reproductive event), while sapling, juvenile and adult distributions were obtained from different reproductive events, conclusions about regeneration processes are tentative because they are based on the limited evidence provided by one census at a single point in time. Although long-term studies are preferable, this type of analysis shows that knowledge of both frugivore behaviour and plant characteristics can be combined to predict seed dispersal by animals and its consequences (Nathan and Muller-Landau 2000).

6. SEED DISPERSAL MODES OF THE SANDSTONE PLATEAU VEGETATION OF THE MIDDLE CAQUETÁ RIVER REGION, COLOMBIAN AMAZONIA[1]

Arbeláez, M.V., and Parrado-Rosselli, A.

ABSTRACT

We characterised the dispersal spectra and phenology of 298 vascular plant species of the sandstone plateaus of Colombian Amazonia. Dispersal modes were determined by the morphology of dispersion units, personal observations on fruit consumption, and an extensive literature review. We obtained the number of species per dispersal mode for the sandstone plateaus and for two recognised vegetation types: open-herbaceous vegetation and low forest-shrub vegetation. Dispersal modes were assigned to 295 plant species. Animals dispersed the highest percentage of species (46.6%), while the percentage of autochorous and anemochorous species was 29.4 and 23%, respectively. The dispersal spectrum of the low forest-shrub vegetation type, based on the coverage of every species, showed that percentages of anemochorous (40.2%) and zoochorous species (37.8%) were similar. Autochory was the most important seed dispersal mode of the open-herbaceous vegetation (60%). Birds were the principal group of potential dispersers (58.9%) of zoochorous species, and reptiles the least important. We found two marked fruiting peaks, one from the end of the dry season to the beginning of the wet season and the second one from the beginning to the middle of the dry season. Our results showed that besides the differences in the vegetation structure and floristic composition between the sandstone plateaus and the adjacent tall forest, there also exist differences in the dispersal spectra and the fruiting rhythms.

RESUMEN

Caracterizamos el espectro de dispersión y la fenología de 298 especies de plantas vasculares de las mesetas de arenisca de la amazonia colombiana. Los mecanismos de dispersión se determinaron con base en la morfología de las unidades de dispersión, observaciones personales sobre el consumo de frutos y una exhaustiva revisión de literatura. Obtuvimos el número de especies por mecanismo de dispersión para las mesetas de arenisca y para los tipos de vegetación reconocidos: vegetación herbácea abierta y vegetación arbustiva-boscosa-baja. Los mecanismos de dispersión fueron asignados a 295 especies de plantas. Los animales dispersaron el mayor porcentaje de especies (46.6%), mientras que el porcentaje de especies autocoras y anemocoras fue de 29.4 y 23%, respectivamente. El espectro de dispersión del tipo de vegetación arbustiva-boscosa-baja, basado en la cobertura de cada especie, mostró que los porcentajes de especies anemocoras (40.2%) y zoocoras (37.8%) son muy similares. La autocoria fue el mecanismo de dispersión de semillas más importante de la vegetación herbácea abierta (60%). Las aves fueron el grupo principal de dispersores potenciales (58.9%) de las especies zoocoras, y los reptiles los menos importante. Encontramos dos picos marcados de fructificación, el primero desde el final de la estación seca hasta el inicio de la estación lluviosa, y el

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segundo desde inicios hasta mediados de la estación seca. Nuestros resultados muestran que además de las diferencias en la estructura de la vegetación y composición florística entre las mesetas de arenisca y el bosque alto adyacente, también existen diferencias en el espectro de dispersión y en los ritmos de fructificación.

Key words: Colombian Amazon; dispersal spectrum; fruiting phenology; open vegetation; sandstone plateaus; seed dispersal.

6.1 INTRODUCTION

The combination of morphological and chemical characteristics of fruits and seeds, and phenological features of plants, so-called dispersal syndromes, are associated with different mechanisms of diaspore dissemination by abiotic or biotic agents such as wind, water, and animals (Gottsberger and Silberbauer-Gottsberger 1983, Howe and Westley 1988, Van der Pijl 1982). The proportion of dispersal modes in a particular vegetation type is defined as the dispersal spectrum, which is influenced by ecosystem attributes, environmental circumstances and floristic composition (Hughes *et al.* 1994, Van der Pijl 1982). Although dispersal syndromes have many exceptions and are moderately predictive about dispersal mechanisms (Fleming *et al.* 1993), knowledge on dispersal spectra of plant communities is helpful for interpreting local ecology and for understanding factors that control composition and structure of ecosystems (Howe and Westley 1988).

Isolated patches of open vegetation occur in tropical rain forests (*e.g.* caatingas, campinaranas, cerrados, and sandstone plateaus of the Guyana Shield; Gottsberger and Morawetz 1986, Huber 1995, Macedo and Prance 1978, Prance 1996). In Colombian Amazonia, sandstone plateaus are located on the western extremes of the Guyana Shield. They consist of a collection of hills, small mountain areas, and savannas mostly found between the Guaviare and Caquetá rivers. Many of these plateaus are built up of horizontally layered sandstone formations of Paleozoic or Mesozoic age, and may rise very high above the lowland landscapes. In most cases, the plateaus form a habitat and substrate for plant communities that are quite different from that of the surrounding tall forest vegetation (Arbeláez and Duivenvoorden 2004). Soils are shallow nutrient-poor white sands (Cuevas 1992), waterlogged in times of rainfall, but drying out quickly during prolonged dry spells (Duivenvoorden and Lips 1993). Plants on the sandstone plateaus are generally of low stature, scleromorphic, and have adapted to a permanent exposure, frequently severe water and high temperature stress, and very low soil nutrient levels (Duivenvoorden and Lips 1993). As such, the sandstone plateaus represent a conglomerate of spatially disjunct patches, characterised by communities that differ substantially in composition and structure from the lowland Amazonian forests (Huber 1988, Maguire 1979, Prance 1996). These differences should also be reflected in their dispersal spectrum. Whereas, 70–90% of plants in tall rain forests have fruits adapted to attract animal seed dispersers (Frankie *et al.* 1974, Gentry 1982, Howe and Smallwood 1982, Howe and Westley 1988), a lower proportion of diaspores dispersed by animals is expected in open vegetation ecosystems, such as the sandstone plateaus, where wind or ballistic dispersal should be more important (Gottsberger and Silberbauer-Gottsberger 1983, Gröger 2000, Splett 1997).

The aims of our study were to characterise the dispersal spectra of the major vegetation types of the sandstone plateaus of the central part of Colombian Amazonia (Figure 6.1), as well as to describe phenological changes of dispersal modes. We were especially interested in answering the following questions: (1) Is the percentage of abiotically dispersed plants (*i.e.* anemochory and autochory) higher than that of animal-dispersed ones? (2) Are the dispersal spectra different among the open-herbaceous and the low forest-shrub vegetation, and between the different strata of the sandstone plateaus? (3) Does the fruiting peak of wind-dispersed plants occur during the dry season, while the fruiting peak of animal-dispersed plants occur during the wet season?

6.2 STUDY SITE

This study was carried out in the sandstone plateaus of the Middle Caquetá River region, states of Amazonas and Caquetá, Colombia (Figure 6.1). Mean annual temperature is 25.7°C, and annual rainfall averages 3060 mm (Duivenvoorden and Lips 1993). Although the region does not have a marked dry season (months with less than 66 mm), rainfall decreases between December and February, while May and June are the wettest months. Sandstone plateaus are one of the four broad landscape units recognized in the Middle Caquetá River region (Duivenvoorden and Lips 1993), and constitute the southernmost sandstone outcrops in the western Amazon basin (Figure 6.1). Around Araracuara, the plateau reaches altitudes of ca 300–350 m a.s.l. Northward, this plateau forms almost a continuum with the Chiribiquete sandstone massive, which rises to ca 900 m a.s.l. (Estrada and Fuertes 1993). Near Araracuara the sandstones pertain to the Araracuara formation, which is of Palaeozoic age (Proradam 1979, Bogotá 1983). The sandstones near Santa Isabel pertain to the Piraparaná Formation of Precambrian origin (Proradam 1979).

Sandstones are characterised by extensive flattened areas, divided by deep crevices and often by the presence of sandstone blocks (Duivenvoorden and Lips 1993). The sandstone is poorly drained, strongly weathered, and lacks most nutrients. Substrate is frequently restricted to the exposed sandstone, which is sometimes partially eroded either to a thin layer of white sand or to a grayish-white soil of sandy texture. All plateaus are surrounded by plains of Tertiary and younger sediments (Duivenvoorden and Lips 1993).

The vegetation of the sandstone plateaus is restricted to the white sand soils and areas with exposed hard rock. Dominant plant families include mostly herbaceous monocots such as Bromeliaceae, Cyperaceae, Eriocaulaceae, Orchidaceae, Poaceae, Rapateaceae, and Xyridaceae, as well as sclerophyllous shrubby dicotyledonous species from the families Apocynaceae, Clusiaceae, Euphorbiaceae, Melastomataceae, and Rubiaceae (Duivenvoorden and Cleef 1994, Arbeláez and Callejas 1999). Arbeláez (2003) recognised two main vegetation types in the study area: the open-herbaceous and the low forest-shrub vegetation. The former is characterised by the presence of early successional species such as *Navia garcia-barrigae*, *Vellozia tubiflora*, and different species of Xyridaceae and Eriocaulaceae. The second vegetation type is dominated by woody species of low stature such as *Bonnetia martiana* and *Gongylolepis martiana*.

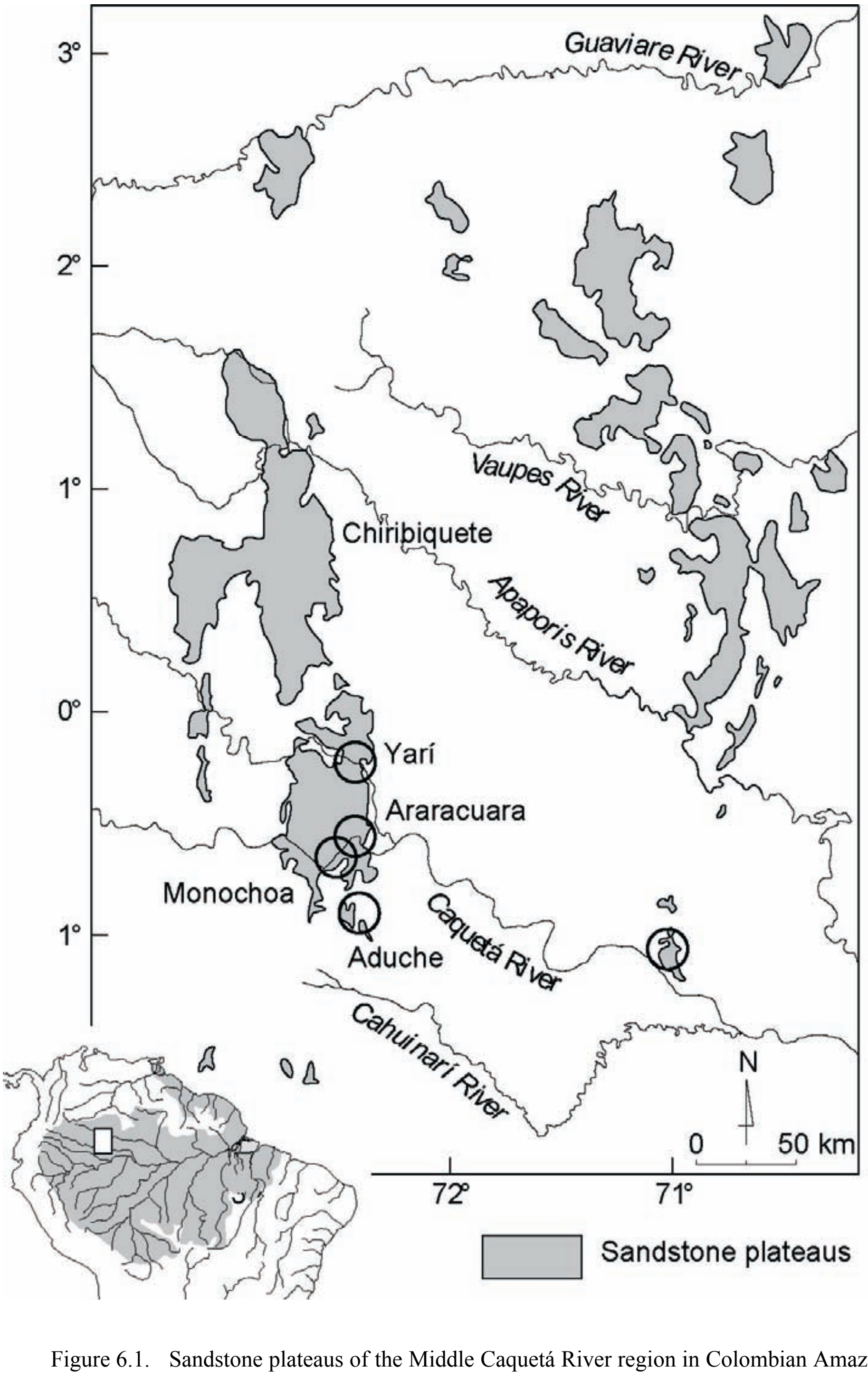

Figure 6.1. Sandstone plateaus of the Middle Caquetá River region in Colombian Amazonia. Circles indicate location of the relevant sites.

Although there is no available information on the local fauna, we have observed typical animals from the tall forest such as tapirs (*Tapirus terrestris*), rats (Muridae), agoutis (*Agouti paca*), acouchis (*Dasyprocta* spp. and *Myoprocta* spp.), and peccaries (*Tayassu pecari* and *Pecari tajacu*) foraging in the open vegetation of this ecosystem. Based on our fieldwork experience and comments of local indigenous people, bats seem to be permanently present in the ecosystem, while primates used to forage in the tall forest and in the transitional phase plateau forest, but not in the open vegetation. Few frugivorous bird species (*i.e. Columba speciosa, Pyrrhura melanura*, *Steatornis caripensis*, *Xenopipo atronitens, Turdus leucomelas*, and *T. ignobilis*) are permanent residents of the sandstone plateaus (Cuadros 1993, Stiles *et al.* 1995). Among reptiles, there are recordings of several species of lizards (Ayala 1986, Sánchez *et al.* 1995), but no turtles have been reported or even observed in this ecosystem.

6.3 METHODS

6.3.1 Vegetation sampling and species identification

During September–December 1996, February–August 1997, February–June 1998, and January–March 1999, we studied plant species composition of sandstone plateaus subdivided over six sites (Figure 6.1) selected on the basis of vegetation maps of Duivenvoorden and Lips (1993). A total of 346 plots of 1–100 m^2 was randomly located in these sites, and sampled according to the French Swiss school relevee method (Mueller-Dombois and Ellenberg 1974). Plot size varied according to general vegetation structure. In each plot, we estimated the percentage cover of vascular plant species. Vouchers of every plant species were collected; most of them were fertile and were determined at the herbaria Amazónico Colombiano (COAH), Nacional Colombiano (COL), Universidad de Antioquia (HUA), Missouri Botanical Garden (MO), Utrecht University (U), and The New York Botanical Garden (NY). Collected vouchers are de-posited in the COAH and HUA and collection numbers correspond to M. V. Arbeláez *et al.* 1-1156.

We classified the fruits of each species into one of ten categories: achene, caryopsis, samara, follicle, legume, capsule, schizocarp, syconia, drupe, and berry (Spjut 1994). The first three categories are dry indehiscent fruits, the next four dry dehiscent fruits, and the last three fleshy fruits. Other fruit categories were not present on the sandstone plateaus. The vegetation was divided into three vertical strata: a lower stratum (0–1 m tall), a middle stratum (1–3 m), and an upper stratum (3 m). Each plant species was assigned to a stratum based on its height independent of its actual growth form (Gottsberger and Silberbauer-Gottsberger 1983). Thus, several species occurred in more than one stratum.

6.3.2 Dispersal modes

Dispersal modes were recorded either by personal observations of fruit consumption events, or deduced from the morphology of the fruits and seeds of collected vouchers and herbarium specimens. Dispersal modes were supplemented with information from previous studies on tropical plants and animals (*e.g.* Ascorra and Wilson 1992, Davidse 1986, Foster *et al.* 1986, Gottsberger and Silberbauer-Gottsberger 1983, Gröger 1995, López and Ramírez 1998, López and Ramírez 1989, Porembski *et al.* 1998, Ramírez 1993, Ramírez *et al.* 1988, Silberbauer-Gottsberger 1984, Snow 1981, Splett 1997, Stevenson *et al.* 2000, Van der Pijl 1982, Van

Donselaar 1965, Van Roosmalen 1985, Wheelwright *et al.* 1984). Each plant species was assigned to one or more dispersal modes. Three dispersal categories were used: autochory, anemochory, and zoochory (Howe and Smallwood 1982, Van der Pijl 1982). Although water may act as a potential form of seed dispersal, we did not find diaspore structures indicating hydrochory. Within autochory, we included both active and passive dispersal. The former involves the explosive liberation of dispersal units, while the latter, which is also called passive ballistic, refers to diaspores released by passing animals, wind, or rain drops (Gottsberger and Silberbauer-Gottsberger 1983). In general, autochorous diaspores were smaller than 2 mm without a conspicuous dispersal structure (Splett 1997). Anemochory was assigned to plants with haired, plumed, or winged dispersal units. We divided zoochorous plants into epizoochory, endozoochory, and myrmechory (Howe and Westley 1988, Van der Pijl 1982). Endozoochory was divided into three groups based on target fruit-eating animals (*i.e.* birds, mammals, and reptiles). Since no rivers pass through the sandstones, fishes were not considered a target group fruit-eating animals. Synzoochory and accidental ingestion of autochorous diaspores by grazing animals were also included in this category (Gottsberger and Silberbauer-Gottsberger 1983). Finally, myrmechory, which is a seed dispersal form rather distinctive from the former two, was assigned to fruits and seeds with an elaiosome or those actively transported by ants.

6.3.3 Fruiting phenology

Fruiting events of each sampled plant species were recorded during the sampling periods mentioned above. Although we tried to visit the six sandstone plateau areas on a regular basis, we could not obtain a complete phenological assessment of all species. Therefore, field observations were confirmed by the examination of all herbarium collections (Borchert 1996) from the sandstone plateau species of the Middle Caquetá River region deposited in the Herbario Amazónico Colombiano (COAH) in Bogotá.

6.3.4 Data analysis

The number of species per dispersal mode was calculated for the sandstone plateaus in general, for each vertical stratum, and for the two vegetation types. Several species can be dispersed by more than one mode, or, in the case of zoochory, more than one group of dispersers. Thus, a proportional value (A) relative to the number of dispersal modes or groups was assigned: A =1 number of modes (Yockteng and Cavelier 1998). Data were expressed in percentages of species relative to the species assigned to a dispersal mode. The relative representation of dispersal modes within the two vegetation types was calculated based on the relative coverage of different species in the vegetation (see Arbeláez 2003). Thus, a relative value of each dispersal mode was obtained by calculating the percentage cover of the species with a dispersal mode: $S_{d,y} = \Sigma\ (A_i \times C_{i,d,y}\ )/\ \Sigma\ C_y$, where $S_{d,y}$ is the share of dispersal strategy d in vegetation type y, A_i is the proportional dispersal value of species i, $C_{i,d,y}$ is cover of species i with dispersal strategy d in vegetation type y, and C_y is the sum of cover of all species in vegetation type y.

6.4 RESULTS

Two hundred ninety-eight vascular plant species were studied in the sandstone plateaus of the Middle Caquetá River region. Dispersal modes could be assigned to

295 species (99%). More than half of the species (164) belonged to the lower stratum. Of these, 114 were exclusively found in this level, 48 were found in the lower and middle strata, while only two were found in all three strata. The middle stratum contained 148 species, but only 51 were exclusive, while 47 also were found in the upper stratum. The upper stratum had 82 species, of which 33 were exclusive.

Capsules, which are dispersed mainly by wind, ballistics, and explosion, were the most abundant fruit type in the overall vegetation, followed by berries and drupes (Table 6.1). Samaras and syconia were the least common fruit types. The low forest-shrub vegetation showed the same pattern. In the open-herbaceous vegetation, capsules also were the most common fruit type, but achenes were more common than fleshy drupes and berries .

Table 6.1. Number and percentage of species per fruit type in the sandstone plateaus of Colombian Amazonia and its two vegetation types: low forest–shrub vegetation and open–herbaceous vegetation

	Sandstone plateaus		Low forest–shrub vegetation		Open-herbaceous vegetation	
Fruit type	No. species	%	No. species	%	No. species	%
Capsule	132	44.3	88	53.7	81	57.9
Berry	50	16.8	28	17.1	13	9.3
Drupe	45	15.1	21	12.8	12	8.6
Achene	27	9.1	9	5.5	14	10.0
Caryopsis	14	4.7	3	1.8	8	5.7
Legume	12	4.0	9	5.5	4	2.9
Follicle	9	3.0	2	1.2	4	2.9
Schizocarp	7	2.3	4	2.4	4	2.9
Samara	1	0.3	-	-	-	-
Syconia	1	0.3	-	-	-	-
Total	298	100	164	100	140	100

6.4.1 Dispersal modes of the sandstone plateaus

Animals dispersed the highest percentage of the sandstone plateau plant species (46.6%; Figure 6.2). Percentage of autochorous and anemochorous plants was 29.4 and 23%, respectively. The percentage of autochorous species decreased from the lower up to the upper stratum, while the percentage of zoochorous species increased (Table 6.2). The highest percentage of anemochorous species occurred in the middle stratum (26.7%). Based on coverage, in the low forest-shrub vegetation type anemochory represented the highest percentage of species (40.2%), followed closely by zoochory (37.8%; Table 6.2). Autochory was the most common seed dispersal mode in the open-herbaceous vegetation (60%) followed by zoochory (22.2%) and anemochory (17.8%; Table 6.2).

Table 6.2. Percentage of plant species per dispersal mode in each vertical stratum, and in the two vegetation types of the sandstone plateaus of Colombian Amazonia

	Dispersal syndrome (%)		
	Anemochory	Autochory	Zoochory
Vertical Strata			
Lower (0-1 m)	23.2	55.8	21.0
Middle (1-3 m)	26.7	7.3	66.0
Upper (>3 m)	17.2	6.0	76.8
Vegetation types			
Low forest–shrub vegetation	40.2	22.0	37.8
Open-herbaceous vegetation	17.8	60.0	22.2

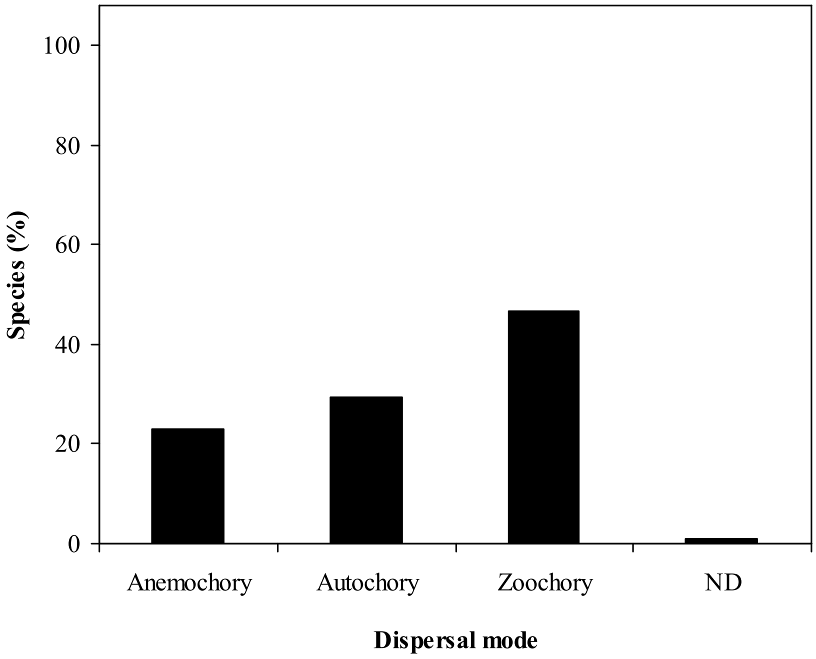

Figure 6.2. Dispersal modes in the sandstone plateaus of Colombian Amazonia. Percentage of species per dispersal mode relative to the total number of plant species studied. ND = undetermined dispersal mode.

6.4.2 Zoochory and groups of potential animal dispersers

Of the 151 zoochorous plant species, 5% were epizoochorous, 12% myrmechorous, and 83% endozoochorous (*i.e.* birds, mammals, reptiles; Figure 6.3). Birds were the principal group of potential dispersers (59%) followed by mammals, while the lowest percentage were reptile-dispersed plants (1%). Regarding zoochory in the vertical strata, bird-dispersed species were dominant in the middle and the upper stratum (Table 6.3). Mammal-dispersed plants were equally common similar in the lower and the upper strata. Epizoochorous plants were exclusively in the lower stratum. Reptile-dispersed plants were absent in the lower stratum, while myrmechorous plants decreased from the lower to the upper stratum.

Table 6.3. Percentage of plant species per animal dispersal mode in each vertical stratum in the sandstone plateaus of Colombian Amazonia.

	Animal dispersal mode (%)				
	Endozoochory (%)				
	Birds	Mammals	Reptiles	Myrmechory	Epizoochory
Vertical Strata					
Lower (0-1 m)	28.5	31.1	0.0	19.4	21.0
Middle (1-3 m)	67.5	15.6	1.6	15.3	0.0
Upper (>3 m)	69.6	26.9	1.2	2.3	0.0

6.4.3 Fruiting phenology

We obtained fruiting data of 267 plant species. In general, we found two marked peaks in the number of fruiting species during the year (Figure 6.4). The highest peak occurred in the beginning of the dry season (October–December), and the second in the end of the dry season (February–March). The lowest number of fruiting species was found in September. May (the wettest month) also showed few fruiting species. Zoochorous and anemochorous species showed a similar trend of variation in the monthly number of fruiting species (Pearson product moment correlation $r = 0.898$, $P < 0.05$). However, temporal fruiting patterns of autochorous species differed from the patterns of zoochorous and anemochorous species (zoochorous $r = 0.517$, $P > 0.05$; anemochorous $r = 0.377$, $P > 0.05$).

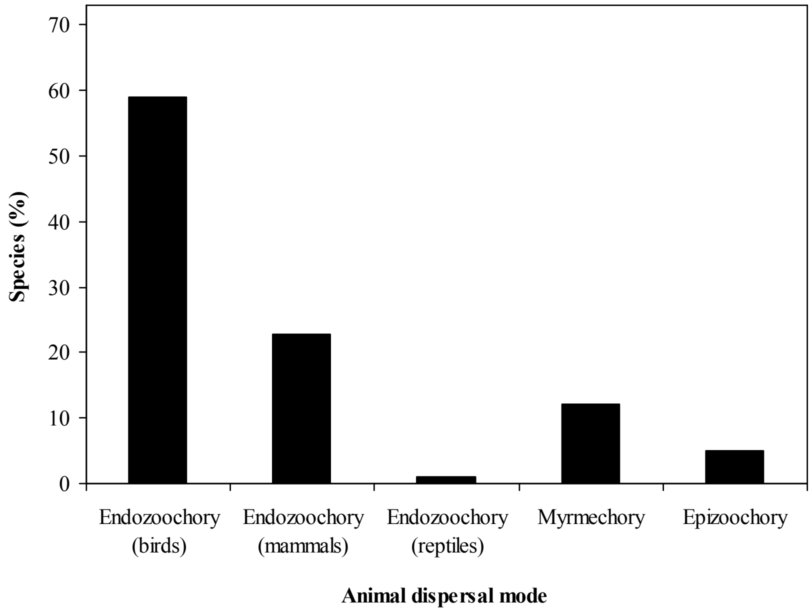

Figure 6.3. Animal dispersal modes in the sandstone plateaus of Colombian Amazonia. Percentage of species per animal dispersal mode relative to the total number of zoochorous species.

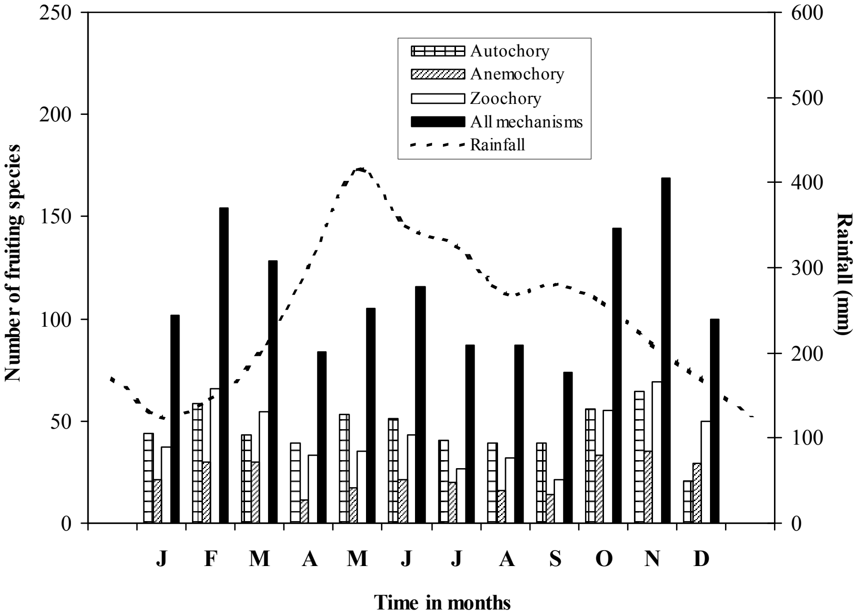

Figure 6.4. Number of fruiting species per month per dispersal mode and the total, being the sum of anemochorous, autochorous, and zoochorous species, in the sandstone plateaus of Colombian Amazonia. Average monthly rainfall (1986–1990; Duivenvoorden and Lips 1993) is represented by a thin continuous line.

6.5 DISCUSSION

As a response to the strong influence of environmental factors and the low density of vertebrates, and probably as an opportunistic way for increasing their chances of survival and maintenance, most of the plants of the sandstone plateaus have more than one mode of dispersal. In the present study, we found that zoochory was the principal dispersal mode of the plants of the sandstone plateaus, but in lower proportion than in the adjacent tall forest, where Castaño (2003) found that 80.5% of plants have fruits adapted for animal dispersal. Abiotic dispersal mechanisms (wind, explosion, and ballistics) are more important in the sandstone plateaus than in the tall forest, where anemochory and autochory range between 15 and 20% (Castaño 2003, Frankie *et al.* 1974, Hilty 1980). Probably, these differences are the consequence of the restricted availability of animal vectors and the open and low stature vegetation of the sandstones that allows greater wind circulation at all height levels.

Although we did not find diaspores with morphological structures indicating hydrochory, the importance of water as a dispersal mechanism in the sandstone plateaus cannot be underestimated. For instance, during flooding periods or during the rainy season, water may act as the proximal form of dispersal of zoochorous, anemochorous, and autochorous species through the action of raindrops, sporadic creeks, or overland flow events. This can be the case of *Utricularia* spp., known for being anemochorous, but commonly growing in wet or swampy areas of the plateaus. Some species of Rapateaceae are also good examples of potentially water-dispersed plants.

Our results are similar to studies on dispersal spectra in related vegetation types (*e.g.* cerrados, caatingas, inselbergs), where zoochory was also the most important mechanism, in combination with considerable amount of abiotic dispersal (more than 20% of the species; Table 6.4). However, in the sandstone plateaus autochory was the second dispersal mode while in the cerrados, caatingas, and restingas, anemochory was second (Gottsberger and Silberbauer-Gottsberger 1983, Griz and Machado 2001, Morawetz 1983). This is probably due to a larger proportion of autochorous grasses found on the sandstone plateaus.

Although we treated every species as individual data points, there are potential biases of assigning dispersal modes. Because of prevalence of a particular dispersal mode within a family, genus, or taxonomic group, species within that group might not be independent because they share a phylogenetic history. Ideally, in order to avoid potential pseudoreplication when comparing the dominance of zoochory, anemochory, or autochory, a phylogenetically independent contrast approach has to be used (Felsenstein 1985). For obtaining independent replicates, however, phylogenies have to be resolved at a level that permits the location of the node of change from one to another dispersal mode, requiring a different approach from the one proposed in this study. Rather than a historical approach, we studied present-day dispersal mechanisms of plants of the sandstone plateaus. Moreover, in case we have made a phylogenetic correction, the 298 species considered share a common local ecological history, for which it is not possible to assess to what extent shared ecological circumstances can be responsible for evolved patterns and if they override the effects of common phylogenetic history. Therefore, we considered that despite this lack of independence due to possible phylogenetic correlations, it is worthwhile to show present-day dispersal spectra of the poorly known sandstone plateaus that will provide a substantial approach on their local and regional ecology.

Table 6.4. Percentage of plant species per dispersal syndrome relative to the total number of species studied in the sandstone plateaus and similar vegetation types of Amazonia. Na: non-available

Ecosystem, location	No species	Dispersal syndrome (%) Autochory [a]	 Anemochory	 Zoochory	Reference
Caatinga, Brazil	42	31	32	36	Griz and Machado 2001
Inselbergs, Venezuela	614	32	29	37	Gröger 2000
Arbustal, Venezuelan Guayana	89	na	49.4	50.5	López and Ramírez 1998
White sand fields, Brazil	390	40	34	21	Splett 1997
Cerrado, Brazil	271	18	30	52	Gottsberger and Silberbauer-Gottsberger 1983
Restringas, Brazil	na	26	31.3	42.7	Morawetz 1983
Campinas, Brazil	37	10.8	13.5	75.7	Macedo and Prance 1978
Sandstone plateaus, Colombia	**298**	**29.4**	**23**	**46.6**	**This study**

[a] Barochory and explosion presented as autochory, following Gottsberger and Silberbauer-Gottsberger (1983).

6.5.1 Dispersal modes in the vertical strata and vegetation types

Analysing the three vertical strata and their dispersal modes, it seems that plant stature and the attributes of the physical environment enhance certain dispersal modes (Gottsberger and Silberbauer-Gottsberger 1983). Animal-dispersed species are predominantly woody, and are dominant in the middle and the upper strata, while autochorous and anemochorous plants are more abundant in the lower stratum. A similar trend occurs regarding the two vegetation types, probably because the presence of both large seeds and animals is associated with closer and taller vegetation. Therefore, in the open-herbaceous vegetation, autochory was the most important dispersal mechanism while zoochory was more important in the low forest-shrub vegetation of the sandstones.

6.5.2 Animal-dispersal (zoochory)

As in other tropical ecosystems, we found that in the sandstone plateaus bird-dispersed fruits outnumber other disperser fruit types (Willson *et al.* 1989). Plant species with zoochorous dispersal may target birds more often than mammals and other animals because of their greater species richness (Willson *et al.* 1989). The low proportion of mammal-dispersed plants might reflect the small crop sizes of such plants, which do not meet the energetic requirements of animals and their risks of being exposed in the open vegetation. Since mammals principally forage in closer and taller vegetation like the sur-rounding tall forest, their importance in seed dispersal relies more on the transport of diaspores from the low forest-shrub vegetation to the tall forest and vice versa. The presence of zoochorus species such as *Clusia spathulaefolia*, *Satyria panurensis*, *Ocotea longifolia*, *Souroubea guianensis*, and *Chrysophyllum sanguinolentum* in both ecosystems can be the result of these dispersal processes.

Animals such as iguanas, lizards, and ants are permanent inhabitants of the sandstone plateaus and can be more abundant than frugivorous birds (Cuadros 1993, Stiles *et al.* 1995). Therefore, they might be more important for seed dispersal than reported in this paper because they have been less studied than other groups of animals and consequently there is less information in the literature. For instance, Griz and Machado (2001) suggested that some plants of caatingas appear to be lizard-dispersed. Gottsberger and Silberbauer-Gottsberger (1983) also reported that in the cerrado vegetation of Brazil, lizards and iguanas eat the same fruits as mammals or even bats. More work needs to be done on the role of ants and reptiles in the seed dispersal processes of the sandstone plateaus.

6.5.3 Fruiting phenology

Sandstone plateaus of Colombian Amazonia differ from the tall forest not only in the floristic composition and the dispersal spectra, but also in the fruiting rhythms of their plants. We found two marked peaks in the number of fruiting species, the first in the beginning of the dry season, and the second in the end of the dry season. Both fruiting peaks coincide with periods of very low fruit availability in the tall forest, where the highest fruit availability occurs during the middle of the rainy season (Castaño 2003; see Chapter 3). Therefore, during fruit scarcity periods in the tall forest, animals would move locally between habitats to feed on the fruits available in the sandstone plateaus.

Although fruiting peaks of the sandstone plateaus may be related to environmental conditions both for dispersal (*e.g.* stronger winds during the dry season) and for germination (first fruiting peak before the wet season starts), zoochorous and anemochorous plant species exhibited similar fruiting patterns. However, these results can be biased because phenological fieldwork recordings were not fully systematically. Thus, supra-annual, annual, and sub-annual species were included within the same year cycle, while fruiting activity of some species was not recorded. Also, while species that are well represented in the herbarium collections reveal actual periods of fruit production, the poorly represented ones do not show reliable fruiting dates (Borchert 1996).

6.5.4 Sandstone plateaus as islands

Island biogeography models proposed by MacArthur and Wilson (1967) state that long distance dispersal is characteristic of island ecosystems such as islands and isolated continental habitats (Anderson 1981, López and Ramírez 1998, Macedo and Prance 1978, Prance 1978, Sugden 1982). Plants with small and light-weighted diaspores, as well as those adapted for bird and wind dispersal may be dispersed over long distances, and are typical of this kind of ecosystems (Macedo and Prance, 1978, Splett 1997, Sugden 1982). Therefore, from a dispersal point of view the sandstone plateaus of Colombian Amazonia can also be considered as biogeographic islands, like the white sand campinas of the Lower Rio Negro region of Brazilian Amazonia (Macedo and Prance 1978). In addition, the species composition between plateaus is similar, but is distinct from that of the surrounding tall forest (Arbeláez 2003, Duivenvoorden and Lips 1993, Huber 1988, Maguire 1979, Prance 1996). Thus, the widespread distribution of typical sandstone species among the scattered spaced sandstone areas can be the result of the existence of remnant populations (Arbeláez and Duivenvoorden 2004), but it can also be the consequence of an effective long distance dispersal.

7. A PARTICIPATORY RESEARCH APPROACH FOR STUDYING FRUIT AVAILABILITY AND SEED DISPERSAL[1]

Parrado-Rosselli, A.

ABSTRACT

In the Middle Caquetá River Region of Colombian Amazonia, the experience of co-operation between the Tropenbos-Colombia Programme and indigenous communities has shown that effective strategies for generating useful information should be developed through participatory research. This paper presents a participatory research approach on fruit availability and seed dispersal with the indigenous community Nonuya of Peña Roja. This approach proceeds in four stages initially with indigenous people as passive field guides progressing to active researchers of the project. The starting point was the distant relationship between scientific and indigenous peoples' knowledge. The first stage (the guide approach) consisted of the participation of indigenous people in a formal scientific research merely as guides, where there was little exchange of knowledge. During the second stage (the field-assistant approach) the guide became a field-assistant, and received training and expertise in scientific methodologies for data collection. In the third stage (from field-assistant to researcher), the indigenous field-assistant realised that it was necessary to know more about nature, his territory, culture, and myths. He proposed his "own research" where he successfully combined both scientific methodologies and dialogue with elders for obtaining information. In the last stage of the process (the researcher approach), information of high-quality and relevance to the needs of indigenous people was generated. In addition, the indigenous researcher learnt more about his own cultures' classification systems, traditions, stories and myths. The interaction between the formal scientists and the indigenous researchers allowed the exchange of experiences, methodologies and learnings, and provided tools for understanding ecological observations and/or cultural beliefs. As a result of this, and previous participatory approaches a direct a common knowledge dialogue between formal scientists and indigenous people has been established in this region of Colombian Amazonia.

RESUMEN

El capítulo 7 presenta una el desarrollo de una investigación participativa sobre oferta de frutos y dispersión de semillas realizada con la comunidad indígena Nonuya de Peña Roja. El proceso se dividió en cuatro etapas que van desde la pasiva participación de los indígenas como guías de campo hasta su activa participación como investigadores. El punto de partida fue una relación distante entre la ciencia occidental y el conocimiento indígena. La primera etapa (guía de campo) consistió en la participación de los indígenas en un proyecto científico formal como guías de campo, en la cual había un escaso intercambio de conocimiento. Durante la segunda etapa (asistente de campo) el guía se convirtió en asistente de campo, y recibió entrenamiento e instrucción en metodologías científicas para la toma de datos. En la tercera etapa (de asistente de campo a investigador), el indígena asistente de campo comprendió que era necesario conocer más acerca de la naturaleza, su territorio,

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[1] Submitted to Ecology and Society as Parrado-Rosselli, A. A participatory approach for studying fruit availability and seed dispersal.

cultura y mitos. El propuso una “investigación propia” en la que combinó exitosamente tanto metodologías científicas como el dialogo con los abuelos para obtener información. En la cuarta etapa del proceso (investigador), se obtuvo información de gran calidad y relevancia a las necesidades de los indígenas. Además, el investigador indígena fue aprendiendo acerca de los sistemas de clasificación indígena, sus tradiciones, historias y mitos. La interacción entre los científicos formales y los indígenas permitió el intercambio de experiencias, metodologías y conocimiento, y proporcionó herramientas para interpretar las observaciones ecológicas y/o los mitos tradicionales. Como resultado de ésta y anteriores trabajos participativos se ha generado un diálogo de saberes directo y más fluido entre la ciencia occidental y el conocimiento indígena en esta región de la amazonia colombiana.

Key words: indigenous peoples’ knowledge, Middle Caquetá River region, Nonuya, seed dispersal, Tropenbos-Colombia, scientific knowledge.

7.1 INTRODUCTION

The importance of indigenous peoples’ knowledge for conservation and management of natural resources has recently been the subject of much of attention (Berkes *et al.* 2000, Huntington 2000). In particular, it has been recognised that the integration of traditional knowledge and western science can result in appropriate resource management strategies (Becker and Ghimire 2003). According to Becker and Ghimire (2003), scientific knowledge offers quantitative biophysical data, information on biodiversity issues, and, hence, a broader appreciation of context beyond the local level. In addition to this, indigenous peoples’ knowledge offers a depth of experience in a local context and a window to cultural interpretations which can be unique and ecologically comparable. From the natural resource conservation perspective, indigenous peoples’ knowledge and scientific knowledge can be complementary.

In the Middle Caquetá River Region of Colombian Amazonia, the experience of the Tropenbos-Colombia Programme (supporting research for conservation and wise use of the tropical forest) over 18 years, have shown that for the adequate understanding and management of biodiversity and natural resources, research should be based on the knowledge and the information needs of the different stakeholders involved (Rodríguez and Van der Hammen 2002, Van der Hammen 2003). Thus, effective strategies and actions for generating useful information should be developed not just from a scientific perspective, but also from a traditional/local perspective using participatory research mechanisms (Rodríguez and Van der Hammen 2002). During the last 10 years of co-operation between Tropenbos-Colombia and indigenous people of the area (or “gente de centro”, as they call themselves based on the point of origin of Andoke, Uitoto, Muinane and Nonuya people), the exclusively scientific research has developed into a combination of local actions, participatory research projects, and the development of “local initiatives” (Rodríguez 2003). The information obtained and its dissemination has formed the basis for the formulation of the natural resource management plans for indigenous peoples’ territories. Although scientific research is still being developed, it has so far not been useful for local communities, either because of its irrelevance to local needs or because communication difficulties between local inhabitants and scientists.

In this paper, I present the process for developing a participatory approach while undertaking scientific research on the role of animals in seed dispersal and spatial distribution of some tree species of terra firme rain forests in Colombian Amazonia. I detail the complete process of this interaction, the information gathered throughout the process, and the achievements made. I discuss the implications of this experience, which can offer useful tools for future work with indigenous communities.

7.2 THE EXPERIENCE IN PEÑA ROJA

The Nonuya people are settled in Peña Roja, located at the western and eastern margin of the Caquetá River, in the Middle Caquetá River region of Colombian Amazonia. Several B.Sc., M.Sc. and Ph.D. research projects have been completed there since 1984, under the support of the Tropenbos-Colombia Programme. Indigenous people have participated within these research projects mainly as guides. In 1997, long-term participatory research proposed by Carlos Alberto Rodríguez, director of the Tropenbos-Colombia Programme, and María Clara Van der Hammen, on forest management by indigenous people was initiated. Important information has been generated both from a scientific and a traditional/local perspective, stimulating an open dialogue between scientists and indigenous people, and providing tools for future participatory work (Rodríguez and Van der Hammen 2002, Van der Hammen 2003).

In 1999, a Ph.D. project entitled "Fruit availability and seed dispersal of common tree species in a terra firme rain forest in Colombian Amazonia" was initiated in the Peña Roja area. Although this was exclusively scientific research, I was aware of the importance of including an indigenous perspective. However, scientific projects are not necessarily interesting and useful for local people, despite the fact that they can generate important information for current scientific discussions on biodiversity and conservation. Recognising the significance of indigenous peoples' knowledge as a system of equal importance to western science, I decided to work in a participatory manner. It was expected that this approach would provide a better understanding of ecological processes and would generate relevant information for indigenous people. Ultimately, this process would stimulate dialogue and knowledge exchange; and would facilitate translation and dissemination of results. The resulting participatory approach was developed in four different stages ranging from locals participating as passive guides to active research participants (Figure 7.1). I describe the general aspects of this process with examples in some cases from my personal experience.

7.2.1. First stage: the guide approach

At the beginning of the project, indigenous people participated merely as guides. They helped in logistics and data collection under direct supervision of the formal scientist. There was little knowledge exchange: the formal scientist provided scientific methodologies for data collection, whilst the indigenous guide provided some basic information about the forest, plants and animals. In general, most of the guides were young men, who had little interest in their traditions and cultural knowledge in part due to the attractions of western society. The potential for knowledge exchange was therefore less than if older men participated.

7.2.2 Second stage: field-assistant approach

In may research projects, the formal scientist hires one or two guides for helping in the data collection. The guide, then, becomes a field-assistant, receiving extra-training and expertise in scientific methodologies for data collection. As a result, the interaction develops into more frequent debates and discussions over observations, findings and interpretations. When this dialogue is stimulated and maintained, both scientist and indigenous field-assistant realise that it is necessary to acquire information for interpreting, understanding and improving the information gathered. Consequently, new and relevant research questions for both knowledge systems may emerge, and should be resolved.

While we were obtaining monthly data on the forest fruit production, several questions arose during discussions on the data obtained and observations. How are the fruiting patterns of the tree species (cultivated and wild) most widely used by the indigenous community? How do patterns vary through time? What are the myths concerning the origin of trees? Do they have an ecological interpretation? Do ecological observations of these tree species have a mythological counterpart?

7.2.3 Third stage: from field-assistant to researcher

As the indigenous field-assistant believed that it was necessary to know more about nature, his territory, culture, and myths, he started to transform into a researcher. In that way, he proposed his "own research" in order to solve some of the questions emerged. In a certain way, this "own research" is within the general framework of "scientific research". No schemes and protocols exist when developing local indigenous research. Thus, methodologies and approaches emerged spontaneously, through discussions, curiosity and experience, and in accordance with the research needs. The indigenous young man had an advantage: he was skilful in scientific methodologies as well as he could dialogue with his elders. Therefore, both methods for generating information were used in methodological design.

"Fruit availability and relationships with seed dispersers of the tree species most widely used by the indigenous community Nonuya of Peña Roja", was the "own research" project title proposed by Jairo Moreno. On the basis of the experience he gained during the field-assistant stage, he applied scientific methodologies for collecting data on the fruiting patterns of the tree species most widely used by the indigenous community (*i.e.* monthly phenological – quantitative and qualitative-censuses of selected individuals of cultivated and wild fruiting trees). As more further information was required, the young indigenous researcher began to be involved with the knowledgeable elders of the community (his father, uncle and two other elders). The dialogue and transmission of knowledge from elders to the young man, involved training and preparation. This had to be a gradual process. The new apprentice-researcher was therefore instructed at the primary level of his peoples' knowledge.

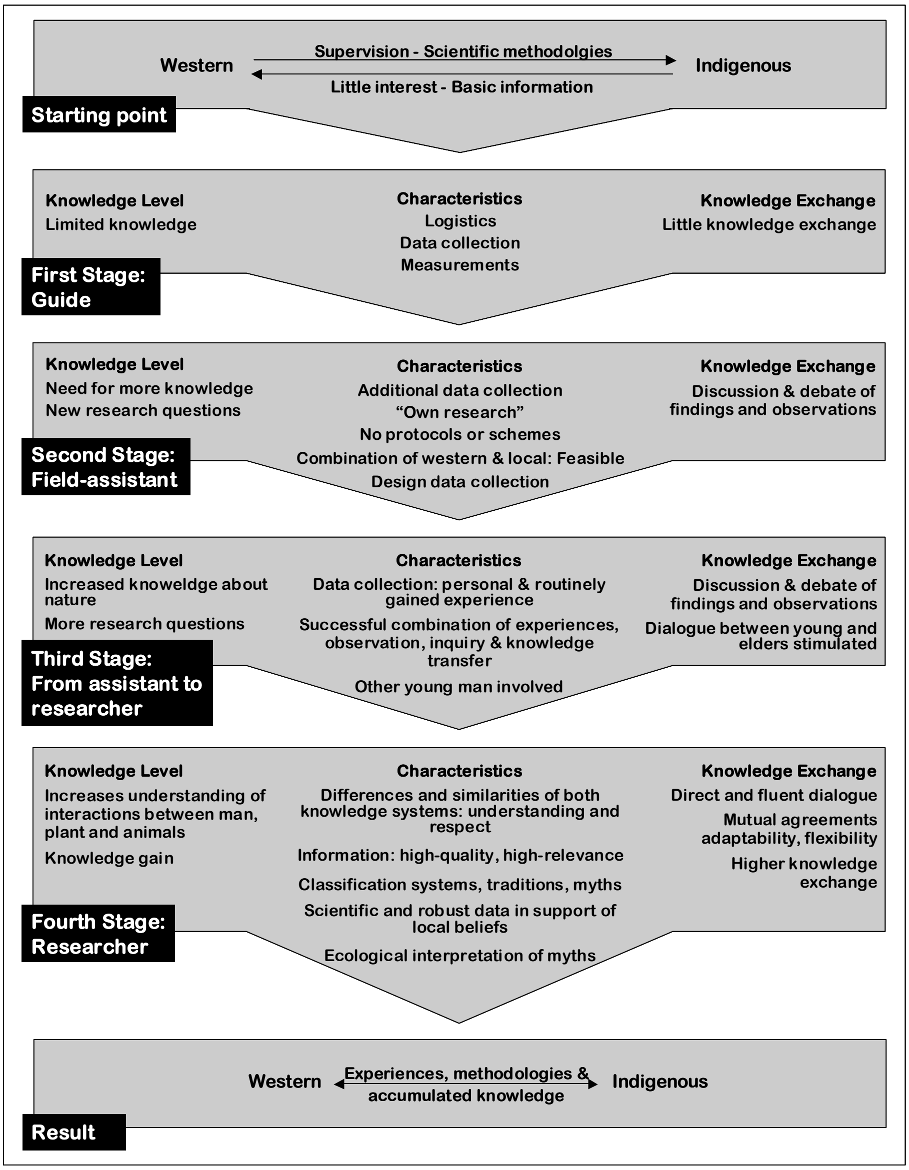


Figure 7.1. Process for developing knowledge exchange through a participatory approach within a research project examining fruit availability and the relationships with seed dispersers of the tree species most widely used by the indigenous community Nonuya of Peña Roja. The starting point of the process is a distant relationship between scientific and indigenous peoples' knowledge. The end state is a closer relationship and a direct interaction between scientific and indigenous knowledge. The stages describe the process of the indigenous people from passive field guides to active researchers participating in the project.

When the indigenous young man began to play an active role in the research process some achievements were made:

1. The indigenous researcher realised that data collection is a personal routinely experience mainly based on observation.
2. Scientific and local (own) methodologies were successfully combined for obtaining information (*i.e.* accumulation of experiences, systematic and casual observations, dialogue with the knowledgeable elders: inquiring, transmission).
3. As other young men started to be involved, the dialogue between youth and elders was stimulated.
4. The indigenous researcher was learning more and more about the interactions between man, plant and animals. Consequently, new and more relevant research questions emerged.

To research further the local knowledge on plant-animal interactions, new questions from the traditional perspective were proposed: What is the relation between the trees studied and their fruit consumers? Is there a special management of frugivores? What are their myths about the origin of the natural world, and do these myths explain our observations?

7.2.4 Fourth stage: researcher approach

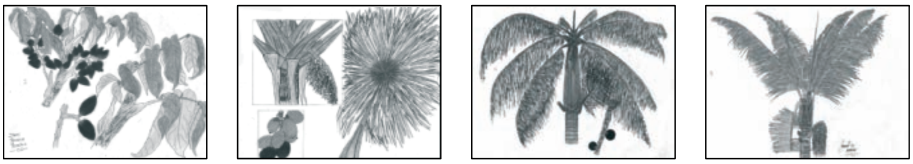
The consolidation of the indigenous young man as a researcher enabled the collection of high-quality information:

Monthly fruit production of 120 fruiting tree species was monitored from June 2000 to September 2002. These species were classified according to the Nonuya classification system, of which 42 were cultivated and 78 wild (Appendix 4). Sixteen groups of fruit-eating animals were also identified, of which, the myth of their origin was obtained. From these groups, 35 species (according to local/traditional classification systems) were birds and 50 were mammals (Appendix 5). Detailed illustrations of all trees and animals studied were made (Figure 7.2). These illustrations provided information for the morphological features of both trees and animals, and have become useful for field identifications.

Also, information of high relevance to the needs of indigenous people was generated:

For the indigenous people of the Middle Caquetá River Region of Colombian Amazonia, or "gente de centro", knowledge on the annual and multi-annual cycles of nature (the so-called ecological calendar), forms the basis for the management of nature and resources in their territories. The ecological calendar is a complex concept that includes seasonality of both biotic and abiotic features. It governs the way of life of indigenous people, influencing cultural and every-day practices such as work, ritual dances, spiritual life, arts, health and education. In this context, the fruiting patterns of plants and their relation to animals are also an important part of the ecological calendar.

FRUITING TREES

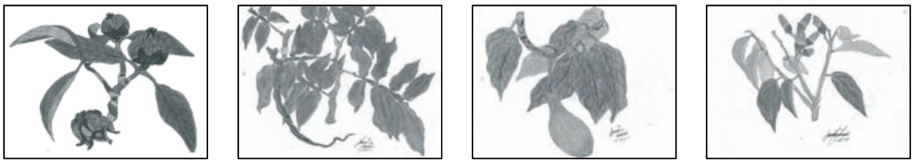


Miya mejegiho
Propio laurel

Uyuta inoo
Canangucho de gusano
lanudo y rojo

Tugu+y+
Asaí común

Cuume
Milpeso común

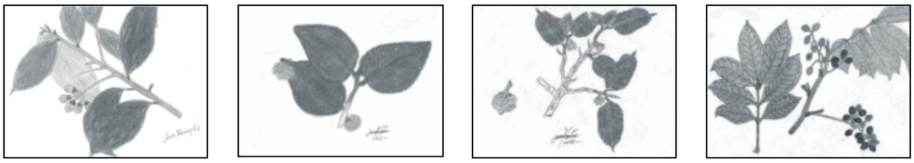


Miya maanio
Breo propio

T+s+o j+gom+ho
Guamo largo
cultivado

Igom+ cuj+
Aguacate de cusumbe

Agey+
Palo rasquiñoso



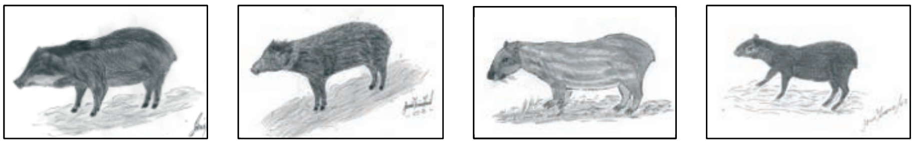
Fat+ba
Palo de guara

K+b+ba
Baco hoja grande y ancha

M+niba
Baco hoja pequeña

Jadijebanoho
Árbol de pepa negra de
pescar

ANIMALS

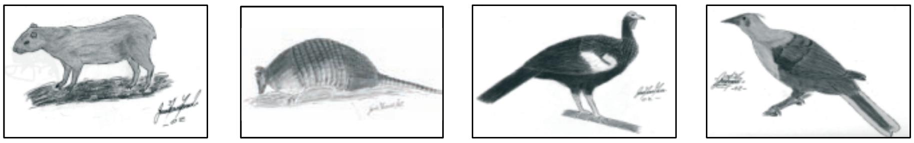


C+bom+ menim+
Puerco pequeño de
cachete blanco
convertido de gente

Samaiba
Cerillo que anda
en par

Jacu Tac+
Borugo de maraca

Fat+gaij+, Fat+
Guara del fruto de
guamo negro



Gue gue J+c+mo
Tintín mediano con
pecho blanco

Jubo go+
Armadillo negro por
encima

Fecaje
Pava cabeza blanco

Cúdi jek+
Mochilero grande que
anda solo pico entre
rojo y anaranjado

Figure 7.2. Example of the illustrations on trees and animals made by Jairo Moreno while undertaking the research project “Fruit availability and relationships with seed dispersers of the tree species most widely used by the indigenous community Nonuya of Peña Roja”, in Colombian Amazonia.

The indigenous researcher learnt more about indigenous peoples' classification systems, traditions, stories and myths. For indigenous people, classification systems, stories and myths can be seen as the symbolic conceptualisation of their interactions with the biotic and abiotic environment. Therefore, they are the basis for understanding and managing health, society and territory. For example, through knowing and relating the story of the origin, and by asking in the appropriate way, the Nonuya have the possibility of managing a plant or an animal for a specific end. Most of these activities have been and are still regulated by knowledgeable elders. For the young man it is just the first step in the process of learning his traditional knowledge.

The origin of plants: Once the creator elder, Mookani had created earth, Mooseji, the creator mother brought in her basket all seeds from all wild plants: large trees, treelets, lianas, herbs, and spread them all over the earth. Mookani, then made the rain fall, and with the rainfall the seeds of the largest trees of the Earth sprouted. Aamehe trees (*Buchenavia tetraphylla*, Combretaceae) were among the earliest ones, and were the predecessors of all plants on earth. Not every seed spread by Mooseji sprouted at the same time. In Nonuya cosmology, the different cultural mythological beings released them at a particular time. Each plant was released by its spiritual owner, who protects and manages the plant. When Mookani created man, he instructed him and gave him the word for taking care, using and managing plants appropriately.

Although the story of the general origin is always the same, some differences in individual stories are found between tribes, ethnic groups and/or clans. The former is the story of the origin of plants for the Mochilero Nonuya clan. For the Gavilán clan, some trees arise from the body of the creator himself: "He transformed his delights and happiness into many cultivated trees. In contrast, he translated all his aches, pains, and troubles into trees, whose physiological features are related or can cause the disease where they come from. For example, "Palo rasquiñoso" (*Endlicheria* spp.; – Lauraceae) comes from the itching in his body, "Palo de guara" (*Licaria guianensis* – Lauraceae) from the headache and a bitter taste in his mouth. When he felt "sticky" he named all the lianas and trees with milky latex, and when he felt "scented" and dizzy he named "Medio comino" (*Ocotea* sp. – Lauraceae)"

Throughout their respective investigations both the indigenous and the formal scientist accumulated knowledge about the forest and the interactions between man, plant and animals. As a consequence, a direct and more fluent knowledge dialogue was established and consolidated. The participatory approach between the western and the indigenous researchers allowed the interaction and exchange of experiences, methodologies and learning, and provided tools for interpreting ecological observations and/or cultural beliefs.

The origin of animals: animals were created after the big flood. El "abuelo de centro", transformed fruits and other foods into different game animals. For example, "Danta de flor blanca" (*Tapirus terrestris*) originated from a combination of fruits; "Cerrillo pequeño que anda en manada" (*Pecari tajacu*) from Miya juvehe (*Poraqueiba* sp.); "Guara de fruto de guamo negro" (*Dasyprocta fuliginosa*) from Fat+gaho (*Parkia panurensis*). Animals transformed from fruits are "true-animals", and man can feed on them without any dire consequences. From the western perspective the animal derived from a particular plant tends to be its main seed disperser.

The direct interaction between the two types of researchers has shown that there are both similarities and differences between knowledge systems. Both sources of understanding rely on direct observation, experience, experimentation, and interpretation. In that way, scientific data obtained may be highly consistent with traditional ecological knowledge on nature:

For the Nonuya, cultivated fruiting trees have their wild equivalents. As said by the "abuelo de centro", cultivating equivalents of wild fruiting trees maintains the reciprocity between man, plants and animals. In addition to morphological features, cultivated species differ from the wild ones in their flowering and fruiting seasons. These differences could also be seen when comparing fruiting patterns of cultivated fruiting trees and fruiting patterns of the forest obtained through scientific methodologies of data recording (Figure 7.3). The fruit production of the forest peaked in the wettest periods of the year, when the fruiting of cultivated trees was very low. The fruiting of cultivated trees peaked in the mid to late-dry season, after the peak of the forest. According to Nonuya, peaking after the highest fruit production of the forest reduces fruit loss and damage of cultivated fruiting trees, as animals will be satiated, and consequently will not be attracted by the cultivated crop. In addition, the fruiting asynchrony enhances seed dispersal processes both by minimising the competition for seed dispersers between ecosystems, and by stimulating local movement of seed dispersers between habitats.

Although both knowledge systems are based on observation experience, the two systems are fundamentally distinct as one is based on abstract traditions (western science), and the other is based on historical traditions (traditional knowledge; Berkes et al. 2000). During the course of our research these differences in world views, cosmology and mechanisms of cultural internalisation were particularly evident in the classification systems:

In this study, the tree and animal species studied also were identified according to western scientific taxonomy. However, many species appeared to be one species in one classification system, while two or more in the other classification systems. For instance, according to western science, in Colombian Amazonia there is only one tapir species (*Tapirus terrestris*) while indigenous people recognise five species of tapirs.

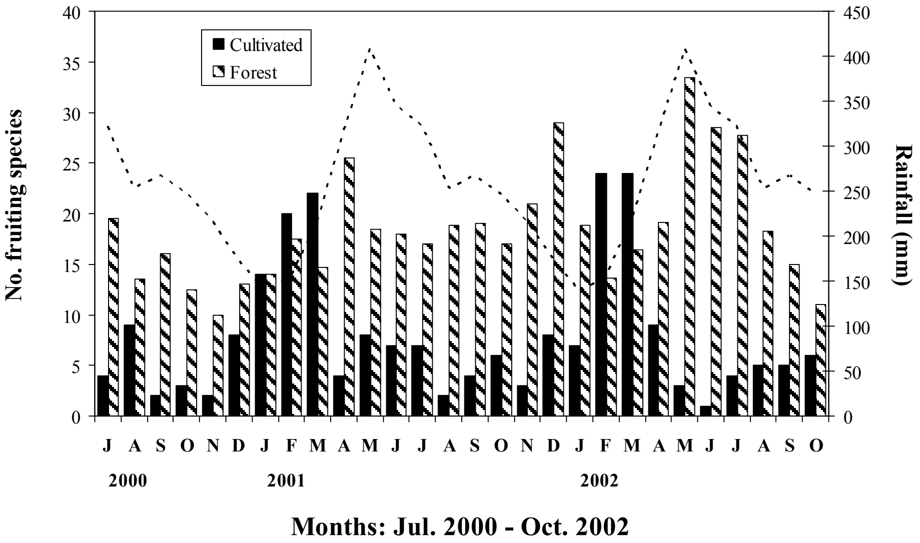


Figure 7.3. Fruiting patterns of cultivated trees and the forest obtained from June 2000 to September 2002 (see Chapter 3), in the Middle Caquetá River region. Mean monthly precipitation (1979-1990; Duivenvoorden and Lips 1993) is represented by a broken line.

Therefore both researchers understood, hence, that not everything can be translated and or interpreted into the other's knowledge system, but must be taken into account and respected. This sets the stage for further participatory processes and research aimed at integrating scientific and indigenous peoples' knowledge.

7.3 LEARNING FROM EXPERIENCE: CONSIDERATIONS

This working experience has provided further evidence that indigenous peoples' knowledge and western science can be complementary. However, participatory research can not be imposed (Rodríguez and Van der Hammen 2002). Participation means taking part, sharing, and being involved. It must be adapted to local conditions, and it has to be formulated in a joint effort between scientific researchers and local inhabitants. Patience, time and permanent discussion and dialogue with local people, mutual agreements, adaptability and flexibility are important tools for achieving participatory research. The success of participatory research lies in understanding each others' time concepts, perceptions, concerns and research needs.

A combination of scientific and indigenous people's knowledge can provide basic and robust information for decision making and for the design of resource management strategies. The participatory process also offers an enriching experience to both indigenous and western participants. Indigenous people have recognised that they are an essential part of nature, and have a responsibility towards the natural world. Hence, they seek to reacquaint themselves with their traditions and knowledge for the control of their territory. Formal scientists have acquired a broader knowledge of plant life-history and evolution, the interactions of animals with their food plants, and how indigenous people optimally manage their territories.

It is essential to continue working towards the recognition of the importance of indigenous peoples' knowledge, and its integration with scientific research. Participatory research schemes may help to restore sustainable land-use practices which indigenous people have used for centuries, and contribute to a direct translation and dissemination of the results of scientific research to local people. New programmes and sustainable conservation strategies can be designed to face the rapidly changing social, economic and biophysical environment. Participatory research can be a valued component of future scientific programmes, particularly conservation-related research projects.

8. GENERAL DISCUSSION

Parrado-Rosselli, A.

There are several issues that can be tackled when studying seed dispersal processes of tropical rain forests, and in the highly diverse forests of Colombian Amazonia. Depending on the perspective from which it is viewed, seed dispersal can give the basic background, clues and information to understand many ecological and evolutionary processes of ecosystems. Based on the research questions proposed, the results presented in this thesis can be summarised in two sections. The first section on fruiting patterns provides answers to the first and the second research questions, while the section on seed dispersal by animals answers the third research question proposed in this project.

8.1 FRUITING PATTERNS

Patterns of fruit production presented in this thesis are characterised by two main facts:

8.1.1 Buffering strategies during periods of low fruit production

It was found that similarly to most tropical communities, the terra firme rain forest of the Tertiary sedimentary plain exhibits seasonal variation in fruit production, peaking in the wettest periods of the year (April to June), while low fruiting periods tend to occur in the late wet and early-mid dry season (October to January; see Chapter 3). During periods of fruit scarcity in this forest site, fruits in other ecosystems and/or fruits of certain plant-guilds become available.

At the ecosystem level it was found that the sandstone plateaus exhibited a contrasting fruiting pattern to the Tertiary sedimentary plain forest. Thus, the highest fruit production in the sandstones occurred in the late wet and mid dry season (October to February), while few species fruited in the wettest periods of the year (see Chapter 6). At the plant-guild level, climbers and epiphytes provided the highest amount of fruit during periods of generalised fruit scarcity in the Tertiary sedimentary plain forest (see Chapter 3). Also, cultivated fruiting trees peaked in the mid and late-dry season, after the peak of the forest, while troughs occurred in the wettest periods of the year, when fruit production in the forest was very high (see Chapter 7).

Animals affected by fruit availability respond by exploiting other plant species and by changing their distribution between forests and habitats. Therefore, the complementary phenological patterns of the vegetation of the sandstone plateaus, climbers and epiphytes, and cultivated fruiting trees might be of critical importance for sustaining frugivore populations during periods of generalised fruit scarcity in the vast Tertiary sedimentary plain forest. Moreover, this can be a strategy for enhancing seed dispersal of either ecosystem or plant-guilds, as competition for seed dispersers is minimised.

8.1.2. Low fruit production in terra firme forests

Fruit production in the extensive terra firme rain forest of the Tertiary sedimentary plain was surprisingly low even during the peak of fruiting season, both in terms of the number of fruits produced and fruit biomass (see Chapter 3). Although hunting activities can be affecting frugivore populations of this region of Colombian Amazonia, the low fruit production largely explains the low frugivore densities observed. As a result of the low animal density in terra firme forests, plants with similar fruiting patterns would compete for seed dispersers. In the case of *Brosimum* and *Dacryodes* (see Chapters 4, 5), the few dispersers available seem to prefer the larger crops of *Brosimum.* Therefore, the low fruit production and the low animal densities can be seen as a limiting seed dispersal factor. The strong competition for the few seed dispersers available can be related to the high tree species diversity observed in these terra firme forests of Colombian Amazonia (Duivenvoorden 1995, 1996; Duque 2004, Duque *et al.* 2003).

8.2 SEED DISPERSAL BY ANIMALS

Two main issues on seed dispersal by animals can be also highlighted from this thesis

8.2.1 Most plant species in tropical rain forests have fruits adapted for animal seed dispersal

Although this fact has been already recognised by several studies carried out in tall tropical rain forests (see Chapters 3, 5, 6), it was surprising to find that in open vegetation ecosystems, such as the sandstone plateaus, zoochory also was the principal dispersal mode (see Chapter 6). However, abiotic dispersal mechanisms (wind, explosion, and ballistics) were more important in the sandstone plateaus than in the tall forest, probably, as a consequence of the substantially different environmental circumstances and the species composition in the open and low stature vegetation of the sandstone plateaus (see Chapter 6). Due to the importance of zoochory in both the sandstones plateaus and the tall forest, the complementarity in their fruiting phenologies would be an important strategy for avoiding competition for seed dispersers.

8.2.2 Seed dispersal by animals for predicting spatial occupation patterns of trees

Results presented in this thesis show that seed dispersal by animals may predict the spatial distribution patterns of tree species with characteristics such as commonness, regular and seasonal fruit production patterns (see Chapter 5). The combined effect of the dispersal agent and seed displacement, resulting in a particular seed shadow, was strongly related to the spatial distribution of subsequent life stages of *Dacryodes* and *Brosimum*. In that way, the clumped distribution of *Dacryodes* adults was consistent with a limited and low seed dispersal, whereas the randomly distributed tree population of *Brosimum* was correlated with high seed dispersal. As only two species were considered in this study, future studies would provide more evidence on the effect of seed dispersal by animals on the spatial patterns of trees. For instance, although not included in this study, data on the spatial distribution of *Pseudolmedia laevis* (Moraceae) in the Amacayacu National Park indicates that this species exhibits a uniform pattern (A. Parrado-Rosselli unpublished data). *Pseudolmedia* is a very common species in these forests, and produces high amounts of fruits in the wettest periods of the year. Consequently, we might expect a high and efficient seed dispersal by frugivores, as well as a significant amount of seeds delivered at long distances from the parent tree. Preliminary observations and reports in the literature have shown that this species is highly consumed mainly by birds of the family Cotingidae, which seem to be high quantity and quality seed-dispersers of the plants on which they feed (Foster *et al.* 1986, Parrado-Rosselli and Amaya-Espinel 2006). Follow up studies, comparisons of larger set of tree species and other forest sites, may show whether predictions are applicable in less diverse forests, under different hunting pressures, or in tropical rain forests on nutrient rich substrate, or whether fruit characteristics such as fruit and/or seed size should be also considered when predicting the effect of animal seed dispersal on spatial patterns of trees in species rich plant community.

8.3 METHODOLOGICAL IMPLICATIONS

8.3.1 Canopy observations

Results presented in this thesis highlight the advantages of conducting observations at the canopy level, particularly to record fruiting patterns, frugivore activity and seed dispersal processes occurring at the highest levels of the forest. We found that the canopy-surveyed plots provided better estimations of habitat-wide fruiting phenology than a the widely used fruit-traps. Surveys from the canopy level, allowed to quantify individual crop sizes and mass, to record availability of both unripe and ripe fruits and their variability over different fruiting periods, and to document fruiting of rare and scarce species hardly detected by other methods (see Chapter 2). In addition, observations on primary seed dispersal made from the canopy, provided more reliable information on animals feeding behaviours, which are often unseen when records are carried out from the ground (see Chapters 4, 5). Thus, direct observations at the canopy level are strongly recommended when quantitative and accurate assessments are needed, not only on fruit production and seed dispersal but also on flower and leaf production.

8.3.2 The participatory research approach

As this Ph.D reserach was carried out in the indigenous community Nonuya of Peña Roja, a participatory research approach was included in order to generate more useful and relevant information for the local community, and to complement the results obtained (see Chapter 7). This participatory research allowed interaction and exchange of experiences, methodologies and learning between western researchers and indigenous people. Moreover, the combination of scientific and indigenous people's knowledge provided a better understanding of the forest ecology and allowed a direct translation and dissemination of the results obtained. It is valuable for future scientific studies to incorporate this kind of approach, since the integration of traditional knowledge and western science can result in more appropriate resource management strategies.

8.4 CONSERVATION IMPLICATIONS

Results presented in this thesis on the fruiting patterns and seed dispersal by animals in the Middle Caquetá River Region, are important to get a better understanding on the factors determining the plant community diversity and structure in these highly diverse forests of Colombian Amazonia. Two aspects that are of main concern to current research trends and conservation strategies in the Colombian Amazon. Future studies on vertebrate and frugivore density, and comparisons with the soil-nutrient rich and higher fruit productive várzea forests will provide an increased understanding of the impacts of seasonal rhythms of fruit supply in animal communities. Also long-term studies with a larger set of tree species can provide more evidence for predicting the effect of seed dispersal by animals on spatial distribution of plants.

Western Amazonian forests are not in danger. Despite the current rates of deforestation in the tropics, the Amazon region is immense and appears to contain viable populations of the vast majority of woody plant species (Duque 2004). Moreover, it is not well known whether frugivore populations have been dramatically depleted in these forests. Subsistence hunting by indigenous people is a millenary activity and it can be seen as a mechanism for maintaining animal populations. However, hunting with commercial proposes has increased during the last years, but studies on animal densities and on the effect of hunting on animal populations are still lacking in his area of Colombian Amazonia. While developing this research I have seen that indigenous people of the Middle Caquetá River region are the main inhabitants and users, but also the principal stewards of the forest. They have developed an extensive knowledge for the management of the biodiversity and resources in their territories. However, during the last years they have been subjected to a strong cultural and language loss. The contact with the western culture, the recent presence of gold miners, drug traffickers and armed groups in the area are affecting them as well as their environment. Thus, biologists and conservationists should work towards the better knowledge of the forests, but also for the recuperation of indigenous people's knowledge by providing them tools for continuing their role as stewards of these forests. Scientific research can provide important information but it must be carried out in combination with indigenous peoples' knowledge, taking into account local research needs. Even more, facts and information must be presented in a language local people can understand.

Finally, many students from Colombian and European universities participated within this research through the study of specific aspects of seed dispersal. This contributed to the organisation of an inter-institutional working group in Colombia mainly focused on plant-animal relationships. Also a group of "canopy people", was created, and nowadays provide support and assessment to people aiming at studying and accessing the Colombian rain forest canopies. Future activities should focus on the consolidation of such working groups in order to integrate and to develop long-term and demand driven research. These activities will increase our knowledge on the complex Amazonian rain forests and will support local communities in the responsible management of their territories.

LITERATURE CITED

Altrichter, M., Drews, C., Senz, J.C. and Carrillo, E. (2002). Presupuesto de tiempo del chancho cariblanco (*Tayassu pecari*) en un bosque húmedo de Costa Rica. *Biotropica* 34: 136-143.

Anderson, A.B. (1981). White-sand vegetation of Brazilian Amazonia. *Biotropica* 13: 199-210.

Arbeláez, M.V. (2003). *Diversity and Dynamics of the Vegetation on Sandstone Plateaus of the Colombian Amazonia.* Ph.D. Thesis, University of Amsterdam, Amsterdam.

Arbeláez, M.V. and Callejas, R. (1999). *Flórula de la meseta de arenisca de la comunidad de Monochoa.* Estudios de la Amazonia Colombiana. XIX. Tropenbos-Colombia. Bogotá.

Arbelaéz, M.V. and Duivenvoorden, J.F. (2004). Patterns of plant species composition on Amazonian sandstone outcrops in Colombia. *Journal of Vegetation Science* 15: 181-188.

Ascorra, C.F. and Wilson, D.E. (1992). Bat frugivory and seed dispersal in the Amazon, Loreto, Peru. *Publicaciones del Museo de Historia Natural* 43: 1-6.

Ayala, S.C. (1986). Saurios de Colombia: lista actualizada, y distribución de ejemplares colombianos en los museos. *Caldasia* 15: 555-575.

Becker, C.D. and Ghimire, K. (2003). Synergy between traditional ecological knowledge and conservation science supports forest preservation in Ecuador. *Conservation Ecology* 8: 1-12 (online) URL:
http://www.consecol.org/vol8/iss1/art1

Berkes, F., Colding, J. and Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* 10: 1251-1262.

Blake, J.G., Loiselle, B.A., Moermond, T.C., Levey, D.J. and Denslow, J.S. (1990). Quantifying abundance of fruits for birds in tropical habitats. *Studies in Avian Biology* 13: 73 – 79.

Bleher, B. and Böhning-Gaese, K. (2001). Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial patterns of seedlings and trees. *Oecologia* 129: 385-394.

Bodmer, R.E. (1991). Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23: 255-261.

Bogotá, J. (1983). Estratigrafía del Paleozóico inferior en el área amazónica de Colombia. *Geología Norandina* 6: 29-38.

Böhning-Gaese, K., Gaese, B.H. and Rabemanantsoa, S.B. (1995). Seed dispersal by frugivorous tree visitors in Malagasy tree species *Commiphora guillaumini*. *Ecotropica* 1: 41-50.

Böhning-Gaese, K., Gaese, B.H. and Rabemanantsoa, S.B. (1999). Importance of primary and secondary seed dispersal in Malagasy tree *Commiphora guillaumini*. *Ecology* 80: 821-832.

Borchert, R. (1996). Phenology and flowering periodicity of neotropical dry forest species: evidence from herbarium collections. *Journal of Tropical Ecology* 12: 65-80.

Borchert, R. (1998). Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change* 39: 381-393.

Botero, P.J., Jiménez, B., Herrera, J.M., Torres, C., Rodríguez, N. Duque, A. and Mendoza, Y. (1999). Análisis fisiográfico sobre la inestabilidad de los paisajes en Orinoquia-Amazonia Colombiana ORAM. *Perspectiva Geográfica* 1: 115-137.

Brewer, S.W. and Webb, M.A.H. (2001). Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos* 93: 32-41.

Brooks, D.M., Bodmer, R.E. and Matola, S. (1997). *Tapirs Status, Survey and Conservation Action Plan.* IUCN Tapirs Specialist Group. IUCN Gland, Switzerland, Cambridge.

Buckley, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. (1993). *Distance Sampling: Estimating Abundances of Biological Populations.* Chapman and Hall, London. 446 pp.

Bustamante, R.O. and Simonetti, J.A. (2000). Seed predation and seedling recruitment in plants: the effect of the distance between parents. *Plant Ecology* 147: 173-183.

Carlo, T.A., Collazo, J.A. and Groom, M. (2003). Avian fruit preferences across a Puerto Rican forested landscape pattern consistency and implications for seed removal. *Oecologia* 134: 119-131.

Castaño-A., N. (2003). *Estimación de la oferta de frutos en el gradiente vertical de un bosque de tierra firme del Medio Río Caquetá, Amazonía colombiana.* BSc. Thesis. Universidad Nacional de Colombia, Bogotá.

Chapman, C., Chapman, L.J., Wrangham, R., Hunt, K., Gebo, D. and Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527- 531.

Chapman, C., Wrangham, R. and Chapman, L.J. (1994). Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160-170.

Chapman, C., Wrangham, R., Chapman, L.J., Kennard, D.K. and Zanne, A.E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15: 189-211.

Clark, D.B., Clark, D.A. and Read, J.M. (1998). Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology* 86: 101-112.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B. Hillerislambers, J., Lichter, J., Mclachlan, J., Mohan, J. and Wyckoff, P. (1999). Interpreting recruitment limitation in forests. *American Journal of Botany* 86: 1-16.

Clark, P.J. and Evans, F.C. (1954). Distance to nearest neighbour as a measure of the spatial relationship in populations. *Ecology* 35: 445-453.

Cleef, A.M. and Arbeláez, M.V. (2005). Diversity and complexity of the Araracuara sandstone flora and vegetation in the Colombian Amazon. *Biologiske Skrifter* 55: 73-87.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest. In: Den Boer, P.J. and Gradwell, G.R. (eds.). *Dynamics of Populations*. Center for Agricultural Publishing and Documentation, Wageningen, pp. 298-312.

Corlett, R.T. and LaFrankie, J.V. (1998). Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change* 39: 439-453.

Cronquist, A. (1981). *An integrated system of classification of flowering plants*. Columbia University Press, New York.

Cuadros, T. (1993). Distribución ecológica de la avifauna de Araracuara (Amazonas). *Revista de ICNE* 4: 15-30.

Cuevas, E. (1992). Relaciones nutricionales de la vegetación de turberas alto-tepuyanas. In: Huber, O. (ed.). *El Macizo de Chimantá*. O. Todtmann, Caracas, pp. 203-218.

Davidse, G. (1986). Fruit dispersal in the Poaceae. In: Soderstrom, T.R., Hilu, K.W., Campbell, Ch.S and Barkworth, M.E. (eds.). *Grass Systematics and Evolution. International Symposium.* Smithsonian Institution Press, Washington, DC., pp. 143-155.

Defler, T.R. (1996). Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagothricha*). *American Journal of Primatology* 38: 289-302.

Defler, T.R. and Defler, S.B. (1996). Diet of a group of *Lagotrix lagothricha lagotricha* in southeastern Colombia. *International Journal of Primatology* 17: 161-190.

Di Fiore, A. (2003). Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology* 59: 47-66.

Donnelly, K. (1979). Simulations to determine the variance and edge-effect of total nearest neighbour distance. In: Hodder, I. (ed.) *Simulation Methods in Archaeology.* Cambridge University Press, London, pp. 91-95.

Duivenvoorden, J.F. (1995). Tree species composition and rain forest-environment relationships in the Middle Caquetá area, Colombia, NW Amazonia. *Vegetatio* 120: 91-113.

Duivenvoorden, J.F. (1996). Patterns of tree species richness in rainforests of the Middle Caquetá area, Colombia, NW Amazonia. *Biotropica* 28: 142-158.

Duivenvoorden, J.F. and Cleef, A.M. (1994). Amazonian savanna vegetation on the sandstone plateau near Araracuara, Colombia. *Phytocoenologia* 24: 197-232.

Duivenvoorden, J.F. and Lips, J.M. (1993). *Ecología del paisaje del Medio Caquetá.* Memoria explicativa de los mapas. Estudios en la Amazonía colombiana. III A-III B. Tropenbos-Colombia, Bogotá. 301 pp.

Duivenvoorden, J.F., Svenning, J.C. and Wright, S.J. (2002). Beta diversity in tropical forests. *Science* 295: 636-637.

Duque, A. (2004). *Plant Diversity Scaled by Growth Forms along Spatial and Environmental Gradients: a Study in the Rain Forests of NW Amazonia.* Ph.D. Thesis University of Amsterdam, Amsterdam, 189 pp.

Duque, A., Cavelier, J. and Posada, A. (2003). Strategies of tree occupation at the local scale in terra firme forests in the Colombian Amazon. *Biotropica* 35: 20-27.

Emmons, L.H. and Feer, F. (1990). *Neotropical Rainforest Mammals: A Field Guide.* University of Chicago Press, Chicago.

Estrada, J. and Fuertes, J. (1993). Estudios botánicos en la Guyana colombiana, IV. Notas sobre la vegetación y la flora de la sierra de Chiribiquete. *Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales* 18: 482-497.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist* 125: 1–15.

Fleming, T.H. (1979). Do tropical frugivores compete for food? *American Zoologist* 19: 1157-1172.

Fleming, T.H., Venable, D.L. and Herrera, L.G. (1993). Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Vegetatio* 107/108: 107-120.

Forget, P.M. (1990). Seed dispersal of *Voucapoua americana* (Caesalpinaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6: 459-468.

Forget, P.M. (1996). Removal of seed of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12: 751-761.

Forget, P.M. Milleron, T. and Feer, F. (1998). Patterns in post-dispersal seed removal by neotropical rodents and seedfate in relation to seed size. In: Newberry, D.M., Prins, H.H.T. and Brown, N.D. (eds.). *Dynamics of Tropical Communities.* Blackwell Science, Oxford, pp. 25-49.

Forget, P.M., Mercier, F. and Collinet, F. (1999). Spatial patterns of two rodent-dispersed rain forest trees *Carapa procera* (Meliaceae) and *Vouacapoua americana* (Caesalpiniaceae) at Paracou, French Guiana. *Journal of Tropical Ecology* 15: 301-313.

Forget, P.M., Hammond, D.S., Milleron, T. and Thomas, R. (2002). Seasonality of fruiting and food hoarding by rodents in neotropical forests: consequences for seed dispersal and seedling recruitment. In: Levey, D.J., Silva, W.R. and Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, Wallingford, pp. 241-256.

Foster, M.S. (1977). Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its food source. *Ecology* 58: 73-85.

Foster, R., Arce, J. and Watcher, T. (1986). Dispersal and sequential plant communities in Amazonian Peru floodplain. In: Estrada, A. and Fleming, T.H. (eds.). *Frugivores and Seed Dispersal*. Dr. W. Junk Publishers, Dordrecht, pp. 357-370.

Foster, R.B. (1982). The seasonal rhythm of fruit fall on Barro Colorado Island. In: Leigh, E.G., Rand, A.S. and Windsor, D.M. (eds.). *The ecology of a tropical forest: seasonal rhythms and long term changes*. Smithsonian Institution Press, Washington D.C., pp. 151-172.

Fragoso, J.M. (1998). Home Range and movement patterns of White-lipped Peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. *Biotropica* 30: 438 - 469.

Frankie, G.W., Baker, H.G. and Opler, P.A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa Rica. *Journal of Ecology* 62: 881-919.

Funch, L.S., Funch, R. and Barroso, G.M. (2002). Phenology of gallery and montane forest in the Chapada Diamantina, Bahia, Brazil. *Biotropica* 34: 40-50.

Galetti, M. and Aleixo, A. (1998). Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology* 35: 286-293.

Galetti, M. and Pedroni, F. (1994). Seasonal diet of capuchin monkey (*Cebus apella*) in a forest in South-east Brazil. *Journal of Tropical Ecology* 10: 27-39.

Galetti, M., Pedroni, F. and Morellato, P.C. (1994). Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil. *Mammalia* 48: 111-118.

Galetti, M., Laps, R. and Pizo, M. (2000). Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic forest of Brazil. *Biotropica* 32: 842-850.

Garwood, N.C. (1982). Seasonal rhythm of seed germination in a semideciduous tropical forest. In: Leigh, E.G., Rand, A.S. and Windsor, D.M. (eds.). *The* *ecology of a tropical forest: seasonal rhythms and long term changes*. Smithsonian Institution Press, Washington D.C., pp. 173-185.

Gautier-Hion, A. (1990). Interactions among fruit and vertebrate fruit-eaters in an African Tropical rain forest. In: Bawa, K.S. and Hadley, M. (eds.). *Reproductive ecology of tropical forest plants*. Man and the Biosphere Series: V.7. UNESCO and The Parthenon Publishing Group, Paris, pp. 219-245.

Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiller, P., Moungazi, A., Roussilhon, C. and Thiollay, J.M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Gayot, M., Henry, O. and Dubost, G. (2004). Comparative diet of the two forest cervids of the genus *Mazama* in French Guiana. *Journal of Tropical Ecology* 20: 31-43.

Gentry, A.H. (1982). Patterns of neotropical plant species diversity. *Evolutionary Biology* 15: 1-84.

Gentry, A.H. (1990). *Four neotropical rainforests.* Yale University Press, New Haven.

Gómez, V. and Maravall, A. (1997). *Programs TRAMO and SEATS, instructions for the user (Beta versión: November 1997).* Working Paper 9628, Research Department, Bank of Spain.

Gottsberger, G. and Morawetz, W. (1986). Floristic, structural and phytogeographical analysis of the savannas of Humaitá (Amazonas). *Flora* 178: 41-71.

Gottsberger, G. and Silberbauer-Gottsberger, I. (1983). Dispersal and distribution in the Cerrado vegetation of Brazil. *Sonderberichten Naturwis. Verein* 7: 315-352.

Griz, L.M. and Machado, I.C. (2001). Fruiting phenology and seed dispersal syndromes in caatinga a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology* 17: 303-321.

Gröger, A. (1995). *Die vegetation der Granit-Inselberge Südvenezuelas: Ökologische und biogeographische Untersuchungen.* PhD Thesis, Botanical Institute, University of Bonn, Bonn.

Gröger, A. (2000). Flora and vegetation of Inselbergs of Venezuelan Guayana. In: Porembski, S. and Barthlott, W. (eds.). *Inselbergs*. Ecological Studies 146. Springer-Verlag Berlin, Heidelberg, pp. 291-314.

Hamill, D. and Wright, S.J. (1986). Testing the dispersion of juveniles relative to adults: a new analytic method. *Ecology* 67: 952-957.

Hammond, D.S. and Brown, V.K. (1998). Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newberry, D.M., Prins, H.H.T. and Brown, N.D. (eds.). *Dynamics of Tropical Communities.* Blackwell Science, Oxford, pp. 51-78.

Hammond, D.S., Brown, V.K. and Zagt, R. (1999). Spatial and temporal patterns of seed attack and germination in a large-seeded neotropical tree species. *Oecologia* 119: 208-218.

Heithaus, E.R., Fleming, T.H. and Opler, P.A. (1975). Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56: 841-854.

Hemingway, C. and Overdorff, D. (1999). Sampling effects on food availability estimates: phenological method, sample size, and species composition. *Biotropica* 31: 354 - 364.

Henry, O. (1999). Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana. *Journal of Tropical Ecology* 15: 292-300.

Herrera, C.M., Jordano, P., López-Soria, L. and Amat, J.A. (1994). Recruitment of mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* 64: 315-344.

Herrera, C.M., Jordano, P., Guitian, J. and Traveset, A. (1998). Annual variability in seed production by woody plants and the masting concept: reassessments of principles and relationship to pollination and seed dispersal. *The American Naturalist* 152: 576-594.

Herrera, L.F., Cavelier, I. Rodríguez, R.C. and Mora, C.S. (1989). *Los alfareros de la Amazonía: el caso de Araracuara.* In: Memorias V Congreso Nacional de Antropología, ICFES, Bogotá, pp. 185–220.

Hilty, S.L. (1980). Flowering and fruiting periodicity in a premontane rain forest in pacific Colombia. *Biotropica* 12: 292-306.

Hilty, S.L. and Brown, W.L. (1986). *A Guide to the Birds of Colombia.* Princeton University Press, Princeton.

Hladik, A. and Mitja, D. (1996). Seedlings, saplings and tree temperaments: potential for agroforestry in the African rain forest. In: Swaine, M.D. (ed.) *The ecology of tropical forest tree seedlings.* Man and the Biosphere Series: V.17. UNESCO and The Parthenon Publishing Group, Paris, pp. 173-192.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. and Tosi, J.A. (1971). *Forest Environments in Tropical Life Zones: A Pilot Study*. Pergamon Press, Oxford.

Hopkins, B. (1954). A new method for determining the type of distribution of plant individuals. Annals of Botany 18: 213-227.

Houle, A.C., Chapman, C. and Vickery, W.L. (2004). Tree climbing strategies for primate ecological studies. *International Journal of Primatology* 25: 237-260.

Howe, H.F. (1982). Fruit production and animal activity in two tropical trees. In: Leigh, E.G., Rand, A.S. and Windsor, D.M. (eds.). *The ecology of a tropical forest: seasonal rhythms and long term changes.* Smithsonian Institution Press, Washington D.C., pp. 189-200.

Howe, H.F. (1990). Seed dispersal by birds and mammals: implications for seedling demography. In: Bawa, K.S. and Hadley, M. (eds.). *Reproductive ecology of tropical forest plants*. Man and the Biosphere Series: V. 7. UNESCO and The Parthenon Publishing Group, Paris, pp. 191-213.

Howe, H.F. (1993). Aspects of variation in a neotropical seed dispersal system. *Vegetatio* 107/108: 149-162.

Howe, H.F. and Estabrook, G.F. (1977). On intraspecific competition for avian dispersers in tropical trees. *The American Naturalist* 111: 817-832.

Howe, H.F. and Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.

Howe, H.F. and Westley, L.C. (1988). Mechanics and ecology of mutualism. In: Howe, H.F. and Westley, L.C. (eds.). *Ecological relationships of plants and animals.* Oxford University Press, Oxford, pp. 107-160.

Hubbell, S.P(1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203: 1299-1309.

Hubbell, S.P. (1980). Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214 - 229.

Hubbell, S.P. (1998). The maintenance of diversity in a neotropical tree community: conceptual issues, current evidence, and challenges ahead. In: Dallmeier, F. and Comiskey (eds.). *Forest Biodiversity Research, Monitoring and Modelling: Conceptual Background and Old World Case Studies.* Man and the Biosphere Series: V. 20. UNESCO and The Parthenon Publishing Group, Paris, pp. 17-44.

Hubbell, S.P. and Foster, R. (1986). Biology, chance and history and the structure of tropical rain forest tree communities. In: Diamond, J.M. and Case, T.J. (eds.). *Community Ecology.* Harper and Row, New York, pp. 314-329.

Huber, O. (1988). Vegetación y flora de Pantepui. *Acta Botanica Brasilera* 1: 41-52.

Huber, O. (1995). Geographical and physical features. In: Steyermark, J.A., Berry, P. and Holst, B.K. (eds.). *Flora of the Venezuela Guayana*. Missouri Botanical Garden, St Louis, Missouri, and Timber Press, Portland, Oregon, pp. 1-61.

Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. and Westoby, M. (1994). Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *Journal of Ecology* 82: 933-950.

Huntington, H.P. (2000). Using traditional ecological knowledge in science: methods and applications. *Ecological Applications* 10: 1270-1274.

Jansen, P.A. and Zuidema, P.A. (2001). Logging, seed dispersal by vertebrates and the natural regeneration of tropical timber trees. In: Fimber, R.A., Robinson, J.G. and Grajal, A. (eds.). *The cutting edge: conserving wildlife in logged tropical forests.* Columbia University Press, New York, pp. 35-59.

Jansen, P.A., Bongers, F. and Hemerik L. (2004). Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* 74: 569-589.

Janzen, D. (1970). Herbivores and the number of tree species in tropical forest. *The American Naturalist* 104: 501 -528.

Janzen, D.H. (1991). *Historia natural de Costa Rica.* The University of Chicago Press, Illinois

Jordano, P. (1992). Fruits and frugivory. In: Fenner, M (ed.). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford, pp. 105-156.

Jordano, P. and Schupp, E.W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb. Ecological Monographs* 70: 591-615.

Kiltie, R.A. (1981). Distribution of palm fruits on a rain forest floor: Why white-lipped peccaries forage near objects. *Biotropica* 13: 141-145.

Korine, C., Kalko, E.K. and Herre, E.A. (2000). Fruit characteristic and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123: 560-568.

Krebs, C.J. (1989). *Ecological methodology.* Harper and Row Publishers, New York.

Levin, S.A., Muller-Landau, H.C., Nathan, R. and Chavé, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution and Systematics* 34: 575-604.

Levine, J.M. and Murrell, D.J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution and Systematics* 34: 549-574.

Lips, J. and Duivenvoorden, J.F. (2001). Caracterización ambiental. In: Duivenvoorden, J.F., Baslev, H., Cavelier, J., Grández, C., Tuomisto, H. and Valencia, R. (eds.). *Evaluación de recursos forestales no-maderables en la Amazonía nor-occidental.* IBED-Universiteit van Amsterdam, Amsterdam, pp. 19-45.

Loiselle, B.A. and Blake, J.G. (1990). Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology* 13: 91-193.

Loiselle, B.A. and Blake, J.G. (1999). Dispersal of Melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* 80: 330-336.

Londoño, C. (2000). *Efecto de la distancia y la densidad en la predación y la remoción de semillas de* Dacryodes chimantensis *(Burseraceae) en la amazonia colombiana.* BSc. Thesis. Pontificia Universidad Javeriana, Bogotá.

Londoño-Vega, A.C. and Alvarez-Dávila, E. (1997). Composición florística de dos bosques (tierra firme y várzea) en la región de Araracuara, Amazonia colombiana. *Caldasia* 19: 431-463.

López, M. and Ramírez, N. (1989). Características morfológicas de frutos y semillas y su relación con los síndromes de dispersión de una comunidad arbustiva de la Guayana Venezolana. *Acta Científica Venezolana* 40: 354-371.

López, M. and Ramírez, N. (1998). Síndromes de dispersión de diásporas de una comunidad arbustiva de la Guayana Venezolana. *Ecotropicos* 11: 15-32.

Lugo, A. and Frangi, J.L. (1993). Fruit-fall in the Luquillo experimental forest, Puerto Rico. *Biotropica* 25: 72-84.

Macarthur, R.H. and Wilson, E.O. (1967). *The theory of island biogeography.* Princeton University Press, Princeton, New Jersey.

Macedo, M. and Prance, G.T. (1978). Notes on the vegetation of Amazonia II. The dispersal of plants in Amazonian white sand Campinas: The Campinas as functional islands. *Brittonia* 30: 203-215.

Maguire, B. (1979). Guayana, region of the Roraima sandstone formation. In: Larsen, K. and Holm-Nielsen, L.B. (eds.). *Tropical botany*. Academic Press, London, pp. 223-238.

Martin, P. and Bateson, P. (1986). *Measuring behavior: an introductory guide*. Cambridge University Press, Cambridge.

Miller, B.W. and Miller, C.M. (2003). *Results of a preliminary survey of the bats of the Mayflower-Bocawina National Park.* Report Wildlife Conservation Society, Belize.

Morawetz, W. (1983). Dispersal and succession in an extreme tropical habitat: coastal sand and xeric woodland in Bahia (Brazil). *Sonderberichten Naturwiss Verein* 7: 359-380.

Morellato, P.C. and Leitão-Filho, H. (1996). Reproductive phenology of climbers in a southeastern Brazilian forest. *Biotropica* 28: 180-191.

Mueller-Dombois, D. and Ellenberg, H. (1974). *Aims and methods of vegetation ecology.* Wiley and Sons, New York.

Munn, C.A. and Loiselle, B.A. (1995). Canopy access techniques and their importance for the study of tropical forest canopy birds. In: Lowman, M and Nadkarni, N.M. (eds.). *Forest Canopies*. Academic Press, San Diego, pp. 165-177.

Nathan, R. and Muller-Landau, H. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends and Ecology and Evolution* 15: 278-285.

Newstrom, L.E., Frankie, G.W. and Baker, H.G. (1994). A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26: 141-159.

Nieder, J., Prosperi, J. and Michaloud, G. (2001). Epiphytes and their contribution to canopy diversity. *Plant Ecology* 153: 51-63.

Palacios, E. and Peres, C.A. (2005). Primate population densities in three nutrient-poor Amazonian terra firme forests of south-eastern Colombia. *Folia Primatol* 76: 135-145.

Palacios, E. and Rodríguez, A. (2001). Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a south-eastern Colombian rainforest. *American Journal of Primatology* 55: 233-251.

Palacios, E., Rodríguez, A and Defler, T. (1997). Diet of a group of *Callicebus torquatus lugens* (Humboldt, 1812) during the annual resource bottle neck in Amazonian Colombia. *International Journal of Primatology* 18: 503-522.

Parrado-Rosselli, A., Cavelier J. and Dulmen Van, A.J.T. (2002). Effect of fruit size on primary seed dispersal of five canopy tree species of the Colombian Amazon. *Selbyana* 23: 245-257.

Parrado-Rosselli, A. and Amaya-Espinel, J.D. (2006). Feeding behavior of the purple-throated fruit crow (*Querula purpurata:* Cotingidae) in the Colombian Amazon and its implications for seed dispersal. *Biotropica* 38, in press.

Peres, C.A. (1994). Primate responses to phenological changes in an Amazonian Terra Firme forest. *Biotropica* 26: 98-112.

Peres, C.A. and Baider, C. (1997). Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in Southeastern Amazonia. *Journal of Tropical Ecology* 13: 595-616.

Pitman, N.C., Terborgh, J.T, Silman, M.R. and Nuñez-Vargas, P. (1999). Tree species distributions in an upper Amazonian forest. *Ecology* 80: 2651-2661.

Porembski, S., Martinelli, G., Ohlemüller, R. and Barthlott, W. (1998). Diversity and ecology of saxicolous vegetation mats on Inselbergs in the Brazilian Atlantic rainforest. *Diversity and Distribution* 4: 107-109.

Prance, G.T. (1978). The origin and evolution of the Amazon flora. *Interciencia* 3: 207-222.

Prance, G.T. (1996). Islands in Amazonia. *Philosophical Transactions of the Royal Society London, Series Biological Sciences* 351: 823-833.

Prieto, T. (2001). *Estudio de la oferta de frutos en un bosque de tierra firme por medio de trampas de frutos y observación desde el dosel en la amazonia colombiana*. BSc. Thesis. Pontificia Universidad Javeriana, Bogotá.

Proradam (1979). *La Amazonía Colombiana y sus Recursos.* Proyecto Radargramétrico del Amazonas. República de Colombia, Bogotá.

Ramírez, N. (1993). Reproductive biology in a tropical shrubland of Venezuelan Guayana. *Journal of Vegetation Science* 4: 5-12.

Ramírez, N., Gil, C., López, M., Hokche, O. and Brito, Y. (1988). Caracterización florística y estructural de una comunidad arbustiva en la Guayana Venezolana (Gran Sabana, Edo. Bolívar). *Acta Científica Venezolana* 39: 457-469.

Rodríguez, C.A. (1999). *Arponeros de la trampa del sol: sustentabilidad de la pesca comercial en el Medio Río Caquetá.* Estudios en la Amazonía colombiana. XVIII. Tropenbos-Colombia, Bogotá.

Rodríguez, C.A. (2003). Proyectos-plata o proyectos-pensamiento. Las iniciativas propias en el Medio Río Caquetá. In: M.V. Rivera (ed.) *Alternativas productivas en la Amazonia colombiana: enfoques y procesos desde lo local.* COAMA, Bogotá, pp. 1-17.

Rodríguez, C.A. and Van der Hammen, M.C. (2002). Participation: stakeholders and the information they need. In: Lawrence, A. and Ambrose-Oji, B. (eds.). *Participatory assessment, monitoring and evaluation of biodiversity (PAMEB),* Environmental Change Institute, University of Oxford, pp. 1-3 (online). URL: http://www.etfrn.org/etfrn/workshop/biodiversity/documents/theme4intro.pdf

Roldán, A.I and Simonetti, J.A. (2001). Plant-mammal interactions in tropical Bolivian forest with different hunting Pressures. *Conservation Biology* 5: 617-623.

Roosmalen Van, M. (1985). *Fruits of the Guianan Flora.* Institute of Systematic Botanic, Utrech University, Netherlands. 483 pp.

Rozo-Mora, M.C. and Parrado-Rosselli, A. (2004). Dispersión primaria diurna de semillas de *Dacryodes chimantensis* y *Protium paniculatum* (Burseraceae) en un bosque de tierra firme de la amazonia colombiana. *Caldasia* 26: 111-124.

Sánchez-C., H., Castaño-M., O. and Cárdenas-A., G. (1995). Diversidad de los reptiles en Colombia. In: Rangel, J.O. (ed.). *Colombia: diversidad biótica I.* Inderena – Universidad Nacional de Colombia, Bogotá, pp. 277-325.

Sánchez-Cordero, V. and Martínez-Gallardo, R. (1998). Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology* 14: 139-151.

Sarmiento, A.M. (1998). *Composición y Distribución de la Fauna Silvestre Utilizada para Cacería en la Comunidad Indígena Andoque y el Asentamiento de Puerto Santander, Medio Río Caquetá, Amazonia Colombiana.* BSc. Thesis. Pontificia Universidad Javeriana, Bogotá.

Schaefer, H.N., Schmidt, V. and Wesenberg, J. (2002). Vertical stratification and caloric content of the standing fruit crop in a tropical lowland forest. *Biotropica* 34: 244-253.

Schnitzer, S.A. and Bongers, F. (2002). The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223-230.

Schupp, E.W. (1990). Annual variation in seedfall, post-dispersal predation, and recruitment of a neotropical tree. *Ecology* 71: 504-515.

Schupp, E.W. (1993). Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Schupp, E.W., Milleron, T. and Russo, S.E. (2002). Dissemination limitation and the origin and maintenance of species rich tropical forests. In: Levey, D.J., Silva, W.R. and Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, Wallingford, pp. 19-33.

Sgarbieri, V.C., Gupte, S.M., Kramer, D.E. and Whitaker, J.R. (1964). *Ficus* enzymes. Part I. Separation of the proteolytic enzymes of *Ficus carica* and *Ficus glabrata* lattices. *Journal of Biological Chemistry* 239: 2170-2177.

Silberbauer-Gottsberger, I. (1984). Fruit dispersal and trypanocarpy in Brazilian Cerrado grasses. *Plant Systematics and Evolution* 147: 1-27.

Silvius, K.M. (2002). Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or "grubivory"? *Journal of Tropical Ecology* 18: 707-723.

Silvius, K.M. and Fragoso, J.M. (2003). Red-rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: implications for the aggregated distribution of forest trees. *Biotropica* 35: 74-83.

Smythe, N. (1970). Relationships between fruiting seasons and seed dispersal methods in a neotropical rain forest. *The American Naturalist* 104: 25-35.

Smythe, N. (1989). Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica* 21: 50-56.

Snow, D.W. (1962). The natural history of the oilbird, *Steatornis caripensis*, in Trinidad, part 2: population, breeding, ecology and food. *Zoologica* 47: 199-221.

Snow, D.W. (1971). Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194-202.

Snow, D.W. (1981). Tropical frugivorous birds and their food plants: A world survey. *Biotropica* 13: 1-14.

Sokal, R.R. and Rohlf, F.J. (1980). *Biometry* (2nd ed.). Freeman, New York, 859 pp.

Spjut, R.W. (1994). *A systematic treatment of fruit types.* New York Botanical Garden, New York.

Splett, S. (1997). *Pflanzenökologische Untersuchungen auf Weißsandfeldern in Zentral- und Südostbrasilien.* Struktur und Diversität einer tropischen Lebensgemeinschaft. Martina Galunder-Verlag, Wiehl.

Statsoft. (1999). *Statistica for Windows*. StatSoft, Inc., Tulsa, USA.

Stevenson, P.R. (2004). Phenological patterns of woody vegetation at Tinigua Park, Colombia: methodological comparisons with emphasis on fruit production. *Caldasia* 26: 125-150.

Stevenson, P.R., Quiñones, M.J. and Ahumada, J. (1998). Annual variation in fruiting pattern using two different methods in a Lowland Tropical forest, Tinigua National Park, Colombia. *Biotropica* 30: 129-134.

Stevenson, P.R., Quiñones, M.J. and Ahumada, J. (2000). Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica* 32: 533-544.

Stevenson, P.R., Quiñones, M.J. and Castellanos, M.C. (2000). *Guía de frutos de los bosques del Río Duda, La Macarena, Colombia*. IUCN, Bogotá.

Stevenson, P.R., Castellanos, M.C., Pizarro, J.C. and Garavito, M. (2002). Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology* 23: 1187-1204.

Stiles, G., Telleria, J.L. and Diaz, M. (1995). Observaciones sobre la composición, ecología y zoogeografía de la avifauna de la Sierra de Chiribiquete, Caquetá, Colombia. *Caldasia* 17: 481-500.

Sugden, A.M. (1982). Long-distance dispersal, isolation, and the cloud forest flora of the Serranía de Macuira, Guajira, Colombia. *Biotropica* 14: 208-219.

Sutton, S.L. (2001). Alice grows up: canopy science in transition from Wonderland to Reality. *Plant Ecology* 153: 13-21.

Svenning, J.C. (2000). Small canopy gaps influence plant-distributions in the rain forest understory. *Biotropica* 32: 252 - 261.

Téllez, P. (2003). *Simulación del ciclo hidrológico en tres tipos de uso del suelo de la Amazonía colombiana.* MSc. Thesis. Universidad Nacional de Colombia, Bogotá.

Terborgh, J.T. (1980). Vertical stratification of a Neotropical forest bird community. *Proceedings of the International XVII Ornithological Congress, Berlin:* 1005-1012.

Terborgh, J.T. (1983). *Five new world primates.* Princeton University Press, Princeton, New Jersey.

Terborgh, J.T. (1990). Seed and fruit dispersal – Commentary. In: Bawa, K.S. and Hadley, M. (eds.). *Reproductive ecology of tropical forest plants.* Man and the Biosphere Series: V.7. UNESCO and The Parthenon Publishing Group, Paris, pp. 181-189.

Terborgh, J.T and Andresen, E. (1998). The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology* 14: 645-664.

Terborgh, J.T. and Van Schaik, C.P. (1987). Convergence vs. non-convergence in primate communities. In: Gee, J.H.R. and Giller, P.S. (eds.). *Organization of communities: past and present.* Blackwell Scientific, Oxford, pp. 205-226.

Terborgh, J.T., Pitman, N., Silman, M., Schichter H. and Núñez, P. (2002). Maintenance of tree diversity in Tropical forests. In: Levey, D.J. Silva, W.R. and Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CAB International, Wallingford, pp. 1-17.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L. and Pollard, J.H. (2002). *Distance 4.0. Release 2.* Rsearch Unit for Wildlike Population Assesment, University of St. Andrews, UK. URL: http://www.ruwpa.st-and.ac.uk/distance/

Tuomisto, H., Ruokolainen, K., Poulsen, A.D., Moran, R., Quintana, C., Caas, G. and Celis, J. (2002). Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia. *Biotropica* 34: 516-533.

Van der Hammen, M.C. (2003). *The indigenous resguardos of Colombia: their contribution to conservation and sustainable forest use.* Netherlands committee for IUCN, Amsterdam

Van der Pijl, L. (1982). *Principles of dispersal in higher plants.* Springer-Verlag, Berlin Third edition.

Van Donselaar, J. (1965). An ecological and phytogeographic study of northern Surinam savannas. *Wentia* 14: 1-163.

Van Roosmalen, M. (1985). *Fruits of the Guianan flora.* Institute of Systematic Botany, Utrecht University, Netherlands, 483 pp.

Van Schaik, C.P., Terborgh, J.T. and Wright, S.J. (1993). The phenology of tropical rain forests: adaptative significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353-377.

Wenny, D.G. (2000a). Seed dispersal of a high quality fruit by specialized frugivores: high quality dispersal? *Biotropica* 32: 327-337.

Wenny, D.G. (2000b). Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monograph*s 70: 331-351.

Wheelwright, N.T. (1985). Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44: 465-477.

Wheelwright, N.T., Haber, W.A., Murray, K.G. and Guindon, C. (1984). Tropical fruit-eating birds and their food plants: A survey of a Costa Rican lower montane forest. *Biotropica* 16: 173-192.

Willson, M.F., Irvine, A.K. and Walsh, N.G. (1989). Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21: 133-147.

Winterhalder, B. and Lu, F. (1997). A forager-resource population ecology model and implications for Indigenous conservation. *Conservation Biology* 11: 1354-1364.

Wright, S.J. and Van Schaik, C.P. (1994). Light and phenology of tropical trees. *The American Naturalist* 143: 192-199.

Wright, S.J, Carrasco, C., Calderón, O. and Paton, S. (1999). The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632-1647.

Wright, S.J., Muller-Landau, H., Calderón, O. and Hernández, A. (2005). Annual and spatial variation in seed fall and seedling recruitment in a neotropical forest. *Ecology* 86: 848-860.

Yockteng, R. and Cavelier, J. (1998). Diversidad y mecanismos de dispersión de árboles de la isla Gorgona y de los bosques húmedos tropicales del pacífico colombo-ecuatoriano. *Revista de Biología Tropical* 46: 45-53.

Zar, J.H. (1984). *Biostatical Analysis.* Second edition. Prentice–Hall, New Jersey.

Zhang, S. and Wang, L. (1995). Comparison of three fruit census methods in French Guiana. *Journal of Tropical Ecology* 11: 281 - 294.

RESUMEN

La dispersión de semillas es el último estadio en el ciclo reproductivo de las plantas, paro a la vez el punto de partida en los procesos de renovación y reclutamiento de la población. La dispersión se semillas determina el rango de expansión, y la estructura espacial y genética de las especies de plantas. Con el fin de entender mejor la ecología y las dinámicas de los bosques amazónicos, se estudiaron algunos aspectos de la dispersión de semillas incluyendo los patrones de producción de frutos y semillas y los mecanismos de dispersión de semillas. La pregunta central de investigación fue cómo los procesos de dispersión de semillas afectan la composición y la estructura de la vegetación de los diversos bosques de tierra firme de la región del medio río Caquetá en la amazonia colombiana.

Los capítulos presentados en esta tesis están organizados y secuenciados temáticamente comenzando con el capítulo introductorio, en el cual se presentan los antecedentes generales para el desarrollo de esta investigación y una descripción del área de estudio. En el capítulo 2, se presenta una metodología mejorada y confiable para el registro de los patrones de producción de frutos. Los capítulos 3 a 6 presentan diferentes aspectos de la producción de frutos y la dispersión de semillas. En el capítulo 7 se muestra el proceso para el desarrollo de una investigación participativa con la comunidad indígena Nonuya de Peña Roja para el estudio de la oferta de frutos y los procesos de dispersión de semillas. El último capítulo (discusión general) conecta los diferentes capítulos presentados. Incluye también algunas recomendaciones para futuros estudios y algunas reflexiones personales acerca de las implicaciones de esta investigación para el mejor conocimiento del bosque, las interacciones entre el hombre, las plantas y los animales, y en consecuencia para la conservación de los bosques tropicales.

En el capítulo 2 el objetivo general fue comparar los datos sobre la fructificación obtenidos simultáneamente a través de trampas de frutos dispuestas en el suelo y de parcelas monitoreadas desde el dosel en un bosque de tierra firme. Los valores procedentes de los monitoreos desde el dosel fueron mayores que los obtenidos con las trampas de frutos. No se encontró relación entre los patrones de fructificación obtenidos a través de los dos métodos. Los resultados mostraron que el método de las trampas de frutos no refleja los patrones de fructificación que ocurren en los estratos más altos del bosque, mientras que las parcelas en el dosel proporcionaron información tanto cuantitativa como cualitativa, y acerca de la contribución de cada especie en la producción de frutos.

El capítulo 3 describe los cambios mensuales en la disponibilidad de fruto para animales a nivel del dosel de un bosque de tierra firme. La fructificación se midió como el número de individuos y de especies en fruto, el número de frutos y su biomasa por mes. Durante 36 meses se registraron 166 especies que ofrecieron frutos adaptados para la dispersión por animales a nivel del dosel. Todas las mediciones mostraron variación estacional en la disponibilidad de frutos, la cual alcanza un pico en los periodos más húmedos del año (Abril a Junio), mientras que los periodos de baja oferta ocurrieron al final de la estación lluviosa y principios de la estación seca (Octubre a Enero). Los árboles y las palmas fueron la forma de crecimiento más importante en la fructificación, principalmente en términos de la

biomasa de frutos. No obstante, las trepadoras y epífitas suministraron la mayor cantidad de fruto durante los periodos de baja producción de las formas arbóreas (final de la estación lluviosa–principios de la estación seca.). Probablemente las trepadoras y epífitas actúan como un recurso alternativo de frutos para los animales, particularmente durante los periodos de escasez. Comparaciones con otros bosques muestran que la producción de frutos en el bosque estudiado es alta respecto el número de especies en fruto, pero muy pobre en las cantidades mensuales y anuales de frutos y biomasa de frutos producidos por hectárea. La baja disponibilidad de frutos parece explicar las bajas densidades de vertebrados en esta región de la amazonia colombiana.

En el capítulo 4 se estudió la dispersión primaria diurna de las semillas de *Dacryodes chimantensis* y *Protium paniculatum* (Burseraceae) en un bosque de tierra firme. Desde diciembre de 1999 hasta junio de 2000 se registraron las visitas de frugívoros, la remoción de frutos y la dispersión primaria de semillas en 5 individuos por especie. Encontramos que *D. chimantensis* presenta en promedio una mayor altura, DAP, área de proyección de la copa y mayores cosechas que *P. paniculatum.* El porcentaje del valor promedio de frutos maduros de *D. chimantensis* osciló entre el 3 y el 21% del tamaño de la cosecha durante toda la estación de frutos, mientras que este porcentaje en *P. paniculatum* varió entre el 1 y 15%. Se observó actividad frugívora diurna en 4 de los 5 individuos de *D. chimantensis* estudiados, mientras que en los individuos de *P. paniculatum* no se presentó frugivoría diurna. Sólo *Amazona festiva* y *A. amazonica* consumieron frutos de *D. chimantensis* y removieron en promedio 1.8 % de los frutos por árbol, pero no alejaron semillas viables del parental (dispersión primaria). En las trampas ubicadas bajo el área de la proyección de la copa sobre el suelo, encontramos que el número de frutos intactos, probados, y dañados por frugívoros fue similar para las dos especies. Las cosechas pequeñas, el número reducido de frutos maduros y las bajas tasas de reducción de la cosecha, sumado un bajo número de visitas, una baja remoción y dispersión primaria diurna de semillas por parte de los frugívoros, sugieren que estas dos especies tienen una dispersión limitada. Se discute el efecto de la baja dispersión por animales en los patrones de distribución espacial de estas especies.

En el capítulo 5 se evaluó el efecto de la dispersión de semillas por animales en los patrones de distribución espacial de *Dacryodes chimantensis* (Burseraceae) y *Brosimum utile* (Moraceae), dos especies de árboles comunes en los bosques de tierra firme de la amazonia colombiana. Para cada una de las especies se registraron los dispersores de semillas y los patrones de deposición de semillas por frugívoros. También se obtuvo la distribución espacial de las semillas y plántulas respecto a los árboles parentales, así como la densidad y la distribución espacial de los juveniles (1–9.99 cm dap) y adultos ($\geq$ 10 cm dap) en un área de 95 ha. Los resultados muestran que la actividad frugívora y la dispersión de semillas por vertebrados fue más alta y más eficiente en *Brosimum* que en *Dacryodes* en términos del número de agentes dispersores, la cantidad y la calidad de sus comportamientos alimenticios, y el número de semillas alejadas del parental. Los tamarinos, tucanes, y roedores fueron los principales dispersores de semillas de *Brosimum,* mientras que no se registraron frugívoros dispersando las semillas de *Dacryodes.* Las distancias de dispersión de las semillas y plántulas de *Dacryodes* respecto al parental (rango:

6.2 – 14.5 m) correspondieron con las distancias de deposición de semillas por animales (aves = 5.1–8.6 m; mamíferos = 4.9–8.3 m), y con la distancia media al vecino mas cercano de juveniles (10.9 m) y adultos (15.4 m). Los adultos y juveniles de *Dacryodes* presentaron un patrón de distribución agregado, con más del 50% de los individuos concentrados a 15 m uno del otro. Las distancias de dispersión de las semillas y plántulas de *Brosimum* concordaron con las distancias de deposición de semillas por aves (8.9–14.0 m) y mamíferos (14.1–18.2 m), con la distribución al azar y las distancias al vecino mas cercano de juveniles (20.2 m) y adultos (25.2 m). Los resultados aquí presentados muestran que a una escala local, la baja dispersión de semillas de *Dacryodes* estuvo correlacionada con la distribución agregada de los árboles en la población, mientras que la alta dispersión de semillas de *Brosimum* estuvo correlacionada con la distribución azarosa de los árboles en la población. El efecto combinado del tipo de frugívoros, su comportamiento alimenticio, y el desplazamiento de semillas por los agentes dispersores parece ser la explicación más apropiada para explicar los patrones observados de la distribución espacial de especies comunes de los bosques de tierra firme de la amazonia colombiana.

En el capítulo 6 el objetivo fue caracterizar el espectro de dispersión y la fenología de 298 especies de plantas vasculares de las mesetas de arenisca de la amazonia colombiana. Los mecanismos de dispersión se determinaron con base en la morfología de las unidades de dispersión, observaciones personales sobre el consumo de frutos y una exhaustiva revisión de literatura. Se obtuvo el número de especies por mecanismo de dispersión para las mesetas de arenisca y para los tipos de vegetación reconocidos: vegetación herbácea abierta y vegetación arbustiva-boscosa-baja. Los mecanismos de dispersión fueron asignados a 295 especies de plantas. Los animales dispersaron el mayor porcentaje de especies (46.6%), mientras que el porcentaje de especies autocoras y anemocoras fue de 29.4 y 23%, respectivamente. El espectro de dispersión del tipo de vegetación arbustiva-boscosa-baja, basado en la cobertura de cada especie, mostró que los porcentajes de especies anemocoras (40.2%) y zoocoras (37.8%) son muy similares. La autocoria fue el mecanismo de dispersión de semillas más importante de la vegetación herbácea abierta (60%). Las aves fueron el grupo principal de dispersores potenciales (58.9%) de las especies zoocoras, y los reptiles los menos importante. Se encontraron dos picos marcados de fructificación, el primero desde el final de la estación seca hasta el inicio de la estación lluviosa, y el segundo desde inicios hasta mediados de la estación seca. Los resultados muestran que además de las diferencias en la estructura de la vegetación y composición florística entre las mesetas de arenisca y el bosque alto adyacente, también existen diferencias en el espectro de dispersión y en los ritmos de fructificación.

El capítulo 7 presenta una el desarrollo de una investigación participativa sobre oferta de frutos y dispersión de semillas realizada con la comunidad indígena Nonuya de Peña Roja. El proceso se dividió en cuatro etapas que van desde la pasiva participación de los indígenas como guías de campo hasta su activa participación como investigadores. El punto de partida fue una relación distante entre la ciencia occidental y el conocimiento indígena. La primera etapa (guía de campo) consistió en la participación de los indígenas en un proyecto científico formal como guías de campo, en la cual había un escaso intercambio de conocimiento. Durante la segunda etapa (asistente de campo) el guía se convirtió en asistente de campo, y recibió entrenamiento e instrucción en metodologías científicas para la toma de datos. En la tercera etapa (de asistente de campo a investigador), el indígena asistente de campo comprendió que era necesario conocer más acerca de la naturaleza, su territorio, cultura y mitos. El propuso una “investigación propia” en la que combinó exitosamente tanto metodologías científicas como el dialogo con los abuelos para obtener información. En la cuarta etapa del proceso (investigador), se obtuvo información de gran calidad y relevancia a las necesidades de los indígenas. Además, el investigador indígena fue aprendiendo acerca de los sistemas de clasificación indígena, sus tradiciones, historias y mitos. La interacción entre los científicos formales y los indígenas permitió el intercambio de experiencias, metodologías y conocimiento, y proporcionó herramientas para interpretar las observaciones ecológicas y/o los mitos tradicionales. Como resultado de ésta y anteriores trabajos participativos se ha generado un diálogo de saberes directo y más fluido entre la ciencia occidental y el conocimiento indígena en esta región de la amazonia colombiana.

En el capítulo final (discusión general) se propone que la combinación entre el tipo de dispersor de semillas y el desplazamiento de las mismas generan una sombra particular de semillas, la cual, a escala local, parece explicar la distribución espacial de las especies de plantas comunes de los bosques de tierra firme. Se plantea además, que los procesos de dispersión de semillas en la región del medio río Caquetá están limitados tanto por la baja producción de frutos como por las bajas densidades de animales. Ante la baja producción de frutos en el extenso bosque de tierra firme del plano sedimentario Terciario, que es particularmente notoria durante ciertos periodos del año, algunos ecosistemas (*i.e.* mesas de arenisca) o grupos de plantas como las trepadoras y epífitas y/o los árboles frutales cultivados responden a través de fenologías de fructificación complementarias. Esta complementariedad, optimiza la dispersión de semillas de estos ecosistemas o grupos de plantas puesto que se minimiza la competencia por dispersores de semillas. Por último, se discute acerca de las metodologías de trabajo utilizadas durante esta investigación: las observaciones desde el dosel del bosque fueron ventajosas para registrar los patrones de fructificación, la actividad frugívora y los eventos de dispersión de semillas que ocurren en los niveles más altos del bosque. La investigación participativa estimuló el diálogo de saberes y el intercambio de conocimiento entre los científicos y los indígenas, y facilitó la diseminación de los resultados de la investigación a nivel local.

SAMENVATTING

Verspreiding van zaden is de laatste stap in de voortplantingscyclus van planten, maar ook het begin van het proces van populatieverjonging en kolonisatie. Zaadverspreiding beïnvloedt de ruimtelijke verbreiding en de ruimtelijke en genetische structuur van plantensoorten. Met het doel een bijdrage te leveren aan de ecologie en dynamiek van de tierra firme bossen van de middenloop van de Caquetá rivier in het Colombiaanse Amazonegebied, heb ik enkele aspecten van zaadverspreiding onderzocht, waaronder patronen van vrucht- en zaadproduktie en mechanismen van zaadverspreiding. De centrale vraag van mijn onderzoek was hoe processen van zaadverspreiding de vegetatiesamenstelling en –structuur van dit soortenrijke deel van het Colombiaanse Amazonegebied beïnvloeden.

De hoofdstukken van dit proefschrift zijn thematisch gerangschikt. De Inleiding geeft de achtergrond van dit onderzoek en een beschrijving van het onderzoeksgebied. Hoofdstuk 2 presenteert een verbeterde en meer betrouwbare methodologie voor registratie van patronen in de vruchtproduktie. Verschillende aspecten van vruchtproduktie en zaadverspreiding worden behandeld in de Hoofdstukken 3 tot en met 6. Hoofdstuk 7 handelt over het proces van onderzoek en kennisuitwisseling met de lokale Nonuya indianengemeenschap uit Peña Roja, ten behoeve van een beter begrip van beschikbaarheid van vruchten en de zaadverspreiding. Het laatste hoofdstuk, de Algemene Discussie, verbindt de voorgaande hoofdstukken. Daarnaast bevat het aanwijzingen voor verder toekomstig onderzoek en persoonlijke gedachten over de implicaties van dit onderzoek voor het begrip van de ecologie van tropische bossen, interacties tussen planten, dieren en de mens, en daarmee voor het behoud van de tropische regenwouden van het Colombiaanse Amazonegebied.

Het doel van Hoofdstuk 2 is de vruchtproduktie, geschat met behulp van op de bosbodem geplaatste vruchtenvallen, te vergelijken met de produktie op basis van visuele schattingen in opnamevlakken in het kronendak. De visuele schatting in de opnamevlakken in het kronendak geeft hogere aantallen dan de schattingen op basis van vruchtenvallen. De patronen, op basis van de verschillende methoden, vertonen geen correlatie. De resultaten laten zien dat de vruchtenvallen-methode de vruchtzettingspatronen, zoals die in de hoogste lagen van het kronendak voorkomen, niet goed weergeven. De kronendak-opnamen geven zowel kwantitatieve als kwalitatieve informatie over de vruchtproduktie in het kronendak, en de bijdragen daartoe van de afzonderlijke soorten.

In Hoofdstuk 3 worden, per maand, de verschillen beschreven van voor dieren beschikbare vruchten in het kronendak van het tierra firme regenwoud. Beschikbaarheid van vruchten is per maand gemeten, en uitgedrukt in het aantal soorten, en aantallen individuen daarbinnen, dat vrucht draagt, het aantal vruchten, en de vruchtmassa. Gedurende 36 maanden zijn in het kronendak 166 soorten gevonden die voor dieren eetbare vruchten dragen. Alle schatters vertonen een seizonale variatie in de beschikbaarheid van vruchten in het kronendak. De hoogste aantallen vruchten werden gevonden in de natte periodes van het jaar (april tot juni), terwijl de produktie van vruchten het laagst is aan het eind van de natte tijd en het begin en midden van de droge tijd (oktober tot januari). Bomen en palmbomen hebben het grootste aandeel in de totale vruchtproduktie, vooral in de totale vruchtmassa. Lianen en epifyten produceren vooral veel vruchten gedurende de periodes waarin bomen een lage vruchtproduktie vertonen (gedurende het eind van de natte tijd en tijdens het begin en midden van de droge tijd). Waarschijnlijk vormen klimplanten en epifyten voor dieren een alternatieve bron van vruchten in tijden van schaarste. In vergelijking met andere gebieden met tropisch regenwoud is het aantal vruchtzettende soorten in het door mij bestudeerde gebied hoog. Daarentegen is het aantal vruchten, per maand en in totaal, en de totale vruchtmassa per hectare laag. De geringe beschikbaarheid van vruchten zou de lage dichtheid van gewervelde dieren in dit deel van het Colombiaanse Amazonegebied kunnen verklaren.

Hoofdstuk 4 behandelt de resultaten van een studie van primaire zaadverspreiding (gedurende de dag) van *Dacryodes chimantensis* en *Protium paniculatum* (Burseraceae). Van december 1999 tot juni 2000 is het bezoek door frugivore dieren, vruchtverwijdering, en primaire zaadverspreiding voor 5 individuele bomen van beide soorten geregistreerd. De gemiddelde boomhoogte, de oppervlakte van de kroonprojectie op de bodem, de diameter van de boomstam op borsthoogte (DBH), en de hoeveelheid vruchten waren alle groter voor *D. chimantensis* dan voor *P. paniculatum*. Tijdens het vruchtseizoen van *D. chimantensis* lag het percentage rijpe vruchten van de totale hoeveelheid vruchten tussen 3 en 21%; voor *P. paniculatum* lag dat tussen 1 en 15%. Frugivore dieren waren overdag actief op 4 van de 5 individuen van *D. chimantensis*, terwijl overdag geen activiteit van frugivoren op *P. paniculatum* is waargenomen. Alleen papegaaien, *Amazona festiva* en *A. amazonica*, aten vruchten van *D. chimantensis*. Per boom verwijderden ze gemiddeld 1,8% van de vruchten, maar transporteerden daarentegen geen levensvatbare zaden van de ouderboom af (primaire zaadverspreiding). De in vruchtenvallen onder de boomkruinen gevonden aantallen intacte, en door dieren beschadigde vruchten, waren voor de beide soorten vergelijkbaar. De lage hoeveelheid vruchten, de lage aantallen rijpe vruchten, en de langzame afname van de hoeveelheid vruchten, gecombineerd met het lage aantal bezoeken, de lage vruchtverwijdering, en geringe zaadverspreiding door frugivoren, suggereren dat het voorkomen van deze twee boomsoorten gelimiteerd wordt door zaadverspreiding. Het effect van een laag aantal door dieren verspreide zaden op de ruimtelijke verbreiding van deze boomsoorten wordt in dit hoofdstuk bediscussieerd.

Het effect van zaadverspreiding door dieren op de patronen van ruimtelijke verbreiding van *Dacryodes chimantensis* (Burseraceae) en *Brosimum utile* (Moraceae) – twee algemene soorten van de tierra firme bossen van het Colombiaanse Amazonegebied – wordt behandeld in Hoofdstuk 5. Bezoek van frugivoren, en patronen van zaaddepositie door deze dieren werd voor beide boomsoorten geregistreerd. In een gebied van 95 ha is de ruimtelijke verbreiding van zaden, zaailingen en jonge boompjes ten opzichte van ouder-bomen opgenomen, evenals de dichtheid en ruimtelijke verbreiding van juvenielen (1-9,99 cm DBH) en volwassen bomen (>10 cm DBH). Activiteit van frugivoren, en zaadverspreiding door gewervelde dieren was hoger en efficiënter voor *Brosimum* dan voor *Dacryodes* in termen van het aantal zaadverspreidende dieren, kwantiteit en kwaliteit van hun foerageergedrag en het aantal zaden dat van de ouder-boom weg getransporteerd werd. Tamarins, toekans en knaagdieren zijn de belangrijkste zaadverspreiders van *Brosimum.* Zaden van *Dacryodes* werden niet door een bepaalde soort, of groep van soorten, verspreid. De afstand tussen zaden, zaailingen en jonge boompjes tot de ouder-bomen van *Dacryodes* (6,2 tot 14,5 m) kwam overeen met afstanden van zadendeposities door dieren (5,1-8,6 m voor vogels; 4,9-8,3 m voor zoogdieren) en met de gemiddelde afstand tussen de dichtstbijzijnde juvenielen (10,9 m) en volwassen bomen (15,4 m). Zowel juvenielen als adulten van *Dacryodes* vertonen een geclusterd verbreidingspatroon: meer dan 50% van de individuen stonden op minder dan 15 m afstand van elkaar. Afstanden van zaden, zaailingen en jonge boompjes voor *Brosimum* (11,0-21,5 m) correspondeerden met afstanden van zaaddeposities door vogels (8,9-14,0 m) en zoogdieren (14,1-18,2 m), met een willekeurig verbreidingspatroon en met de afstanden tussen de dichtstbijzijnde juvenielen (20,2 m) en volwassen bomen (25,2 m). Uit de resultaten blijkt dat – op lokale schaal – de lage graad van zaadverspreiding gecorreleerd is met een geclusterd ruimtelijk verbreidingspatroon voor *Dacryodes*. De hoge graad van verspreiding van *Brosimum* komt overeen met het willekeurig verbreidingspatroon van de individuen in de populatie. Waarschijnlijk bepaalt de combinatie van een aantal factoren, namelijk het type frugivoor, hun voedingsgedrag, en het transport van de zaden, de waargenomen ruimtelijke patronen van de algemene boomsoorten in de tierra firme bossen van het Colombiaanse Amazonegebied.

Hoofdstuk 6 presenteert spectra van zaadverspreiding en fenologie van 298 soorten van vaatplanten van de zandsteenplateaus van het Colombiaanse Amazonegebied. Wijzen van zaadverspreiding van de verschillende soorten zijn afgeleid van de morfologie van de verspreidingseenheid, observaties van vruchtconsumptie, en van een grondige literatuurstudie. Het aantal soorten per verspreidingswijze is voor twee vegetatietypen van de zandsteenplateaus opgenomen: een open kruidachtige vegetatie, en een lage bos-struik-achtige vegetatie. Voor 295 plantensoorten werd de verspreidingswijze vastgesteld. Het percentage zoöchore (dierverspreide) soorten is het hoogst (46,6%); voor autochore (verspreid met een “werpmechanisme”) en anemochore (windverspreide) soorten is dat respectievelijk 29,4 en 23,3%. Het zaadverspreidingsspectrum van de bos-struik-achtige vegetatie, gebaseerd op bedekkingspercentages van de soorten, laat zien dat de percentages voor anemochorie en zoöchorie overeenkomen: respectievelijk 40,2 en 37,8%. Autochorie is de belangrijkste verspreidingswijze voor de open kruidvegetatie (60%). Vogels vormen de voornaamste groep van potentiële verspreiders van zoöchore soorten (58,9%) en reptielen de minst belangrijke. Er zijn twee opvallende pieken in de vruchtzetting gevonden: één van het eind van het droge seizoen tot het begin van het natte seizoen, en de tweede piek van het begin tot het midden van het droge seizoen. Naast verschillen in vegetatiestructuur en floristische samenstelling tussen de zandsteenplateau’s en het naburige hoge regenwoud, bestaan er dus ook verschillen in verspreidingsspectra en het moment van vruchtzetting.

In Hoofdstuk 7 wordt verslag gedaan van een participatieve aanpak van onderzoek naar de beschikbaarheid van vruchten en zaadverspreiding, waarbij de kennisuitwisseling met de Nonuya-indianengemeenschap van Peña Roja centraal stond. De ontwikkeling hiervan verliep in vier fasen: van passieve gids in de beginfase tot actieve onderzoeker in de laatste fase. In de beginsituatie was er sprake van een grote afstand tussen de kennis van de wetenschappelijke onderzoeker en die van de inheemse gids. In de eerste fase (de “gidsfase”) werkten de indianen voornamelijk als gids mee aan het wetenschappelijk onderzoek, waarbij er weinig uitwisseling van kennis was. De tweede fase (de “veldassistent-fase”) begon toen er sprake was van training van de assistent in wetenschappelijke methoden van gegevensverzameling, en het verkrijgen van ervaring daarmee. Gedurende de derde fase (van veldassistent naar onderzoeker) realiseerde de inheemse veldassistent zich dat zijn kennis over de natuur, zijn land, cultuur en mythen noodzakelijkerwijs vergroot moest worden. Hij stelde een “eigen onderzoek” voor, waarin ten behoeve van de dataverzameling wetenschappelijke methoden succesvol werden gecombineerd met dialogen met de ouderen. De vierde, en laatste, fase (de “onderzoeker-fase”) werd gekenmerkt door het genereren van hoogkwalitatieve informatie, die aansluit op de behoeften van de lokale bevolking. Daarbij deed de inheemse onderzoeker kennis op over de classificatiesystemen, tradities, verhalen en mythen van zijn eigen cultuur. De interactie tussen wetenschappers en inheemse onderzoekers zorgde voor uitwisseling van ervaring en methodologie, en maakte het makkelijker ecologische observaties en culturele opvattingen te begrijpen. Dit proces heeft, samen met eerdere projecten met participatie van de indianen, gezorgd voor een directe en frequente kennisuitwisseling tussen wetenschappers en indianen in dit deel van het Colombiaanse Amazonegebied.

In de Algemene Discussie stel ik dat de combinatie van het effect van het zaadverspreidende dier, en van transport van zaden, resulteert in een bepaalde zaadschaduw. Dit kan de ruimtelijke verbreidingspatronen van de meest voorkomende plantensoorten van het tierra firme bos op lokale schaal verklaren. Daarbij geloof ik dat zaadverspreiding in het gebied van de middenloop van de Caquetá rivier gelimiteerd wordt door een lage produktie van vruchten, en lage dichtheden van fauna. Vooral in bepaalde perioden van het jaar wordt de lage vruchtproduktie gecompenseerd door een tijdelijk hogere vruchtproduktie in andere, naburige, ecosystemen (zandsteenplateaus), of in andere groepen van planten (epifyten en klimplanten). Bovendien zorgt deze ruimtelijke spreiding van vruchtzetting ervoor dat de competitie tussen boomsoorten om zaadverspreidende dieren lager is, hetgeen een betere zaadverspreiding voor die boomsoorten tot gevolg heeft. In het laatste hoofdstuk bediscussieer ik de methodologieën die voor dit onderzoek gebruikt zijn. Registratie van patronen van vruchtzetting, frugivorie-activiteit, en processen van zaadverspreiding kunnen beter gedaan worden met behulp van kronendak-observaties. Een participatieve onderzoeksaanpak heeft de uitwisseling van kennis tussen wetenschappers en de inheemse bevolking bevorderd. Dit is de verspreiding van onderzoeksresultaten onder de inheemse bevolking ten goede gekomen.

SUMMARY

Seed dispersal is the last step in the reproductive cycle of plants, but also the starting point in the process of population renewal and recruitment. Seed dispersal determines the expansion range, and the spatial and genetic structure of plant species. Aimed at better understanding of the ecology and dynamics of Amazonian rain forests, some aspects of seed dispersal, including fruit and seed production patterns, and mechanisms of seed dispersal were investigated. The central question of this research was how seed dispersal processes affect the vegetation composition and structure of the highly diverse terra firme rain forests of the Middle Caquetá River region of Colombian Amazonia.

The chapters presented in this thesis are arranged in a thematic progression beginning with an introductory chapter, where general background for developing this research and a description of the study area are presented. Chapter 2 reports an improved and reliable methodology for recording fruit production patterns. From Chapters 3 to 6 different aspects of fruit production and seed dispersal are reported. Chapter 7 presents the process of developing a participatory research approach with the indigenous community Nonuya of Peña Roja for understanding fruit availability and seed dispersal. The last chapter (general discussion) serves as a bridge between the different chapters presented. It also includes directions for future work and personal thoughts on the implications of this research for the better understanding of the forest ecology, the interactions between man, plant and animals, and hence, for the conservation of tropical rain forests.

In Chapter 2 the objective was to compare fruiting data derived simultaneously from fruit-traps placed on the ground and from canopy-surveyed plots in a terra firme rain forest site. Values derived from the canopy-surveyed plots were higher than fruit-trap estimates. Fruiting patterns obtained throughout both methods were not correlated. The results showed that the fruit-trap method does not accurately reflect fruiting patterns occurring at the highest levels of the forest, while the canopy-surveyed plots provided both quantitative and qualitative information on the canopy fruit production, and each species contribution.

Chapter 3 describes monthly changes in fruit availability for animals at the canopy level in a terra firme rain forest site. Fruit availability was measured as the number of individuals and species bearing fruits each month, the number of fruits and the amount of fruit mass per month. After 36 months, 166 species bearing fruits adapted for animal seed dispersal were recorded at the canopy level. All estimates showed seasonal variation in canopy-fruit availability, peaking in the wettest periods of the year (April to June), while low fruiting periods occurred in the late wet and early-mid dry season (October to January). Trees and palms were the most important fruiting growth form, particularly in terms of fruit mass. Nevertheless, climbers and epiphytes provided most of the fruits during low fruiting periods of arboreal growth forms (late wet and early-mid dry season). Probably, climbers and epiphytes serve as an alternative fruit resource for animals, particularly during periods of fruit scarcity. Comparison with other tropical rain forests showed that fruit production in the forest studied is high in the number of fruiting species, but very poor in the monthly and total number of fruits, and in the fruit mass produced per hectare. The low fruit

availability seems to explain the low vertebrate densities in this region of Colombian Amazonia.

In Chapter 4 diurnal primary seed dispersal of *Dacryodes chimantensis* and *Protium paniculatum* (Burseraceae) was studied in a terra firme rain forest site. From December 1999 to June 2000 frugivore visits, fruit removal and primary seed dispersal were recorded in 5 individuals per species. Mean tree height, area of canopy projection, diameter at breast height (dbh), and fruit crop sizes of *D. chimantensis* were found to be larger than in *P. paniculatum.* During the fruiting season of *D. chimantensis,* mean percentage of ripe fruits relative to the fruit crop size ranged between 3 and 21%, while percentage of ripe fruits of *P. paniculatum* ranged between 1 and 15%. Diurnal frugivore activity was observed in 4 out of the 5 individuals of *D. chimantensis,* while no diurnal frugivory was observed in the *P. paniculatum* individuals. Only the parrots *Amazona festiva* and *A. amazonica*, fed on *D. chimantensis* fruits. They removed an average of 1.8% fruits per tree, but they did not carry away viable seeds from the parent tree (primary seed dispersal). In the traps located under the area of canopy projection, the number of intact fruits, picked and damaged by animals was similar for both species. The small fruit crop sizes, the low number of ripe fruits and the low rate of fruit crop reduction, together with the low number of visits, fruit removal and diurnal primary seed dispersal by frugivores suggest that these two species are dispersal limited. The impact of the low seed dispersal by animals on the spatial distribution patterns of these tree species is discussed.

In Chapter 5 it was evaluated the effect of seed dispersal by animals on the patterns of spatial distribution of *Dacryodes chimantensis* (Burseraceae) and *Brosimum utile* (Moraceae), two common tree species of terra firme rain forests of Colombian Amazonia. Animal seed dispersers and patterns of seed deposition by frugivores were recorded for each tree species. The spatial patterns of seed, seedling and sapling distribution relative to parent trees were obtained. In addition, the density and spatial distribution of juveniles (1 – 9.99 cm dbh) and adult trees ($\geq$ 10 cm dbh) were recorded throughout a 95 ha area. The results showed that frugivore activity and seed dispersal by vertebrates was higher and more efficient in *Brosimum* than in *Dacryodes* in terms of the number of animal dispersers, the quantity and quality of their feeding behaviours, and the number of seeds transported away from the parent tree. Tamarins, toucans, and rodents were the main dispersers of *Brosimum* seeds, while no particular species or set of frugivores dispersed *Dacryodes* seeds. Dispersal distances of *Dacryodes* seeds, seedlings, saplings away from the parent tree (range: 6.2 – 14.5 m) were consistent with distances of seed deposition by animals (birds = 5.1 – 8.6 m; mammals = 4.9 – 8.3 m), and with the mean nearest neighbour distance of juveniles (10.9 m) and adults (15.4 m). Both *Dacryodes* juveniles and adults exhibited a clumped distribution pattern, with more than 50% of individuals being within 15 m of each other. Dispersal distances of *Brosimum* seeds, seedlings and saplings (11.0 – 21.5 m) corresponded well with distances of seed deposition by birds (8.9 – 14.0 m) and mammals (14.1 – 18.2 m), with the random distribution pattern and nearest neighbour distances of juveniles (20.2 m) and adults (25.2 m). The results presented here showed that on the local scale, the low dispersal *Dacryodes* was correlated with a clumped tree population, whereas the high seed dispersal of *Brosimum* was correlated with a randomly distributed tree population.

The combination of the type of frugivores, their feeding behaviour, and the seed displacement by all seed dispersal agents seem to be the most likely explanation for the observed spatial patterns of common tree species in the terra firme rain forests of Colombian Amazonia.

In Chapter 6 the objective was to characterise the dispersal spectra and phenology of 298 vascular plant species of the sandstone plateaus of Colombian Amazonia. Dispersal modes were determined by the morphology of dispersion units, personal observations on fruit consumption, and an extensive literature review. The number of species per dispersal mode for the sandstone plateaus was obtained, as well as for two recognised vegetation types: open-herbaceous vegetation and low forest-shrub vegetation. Dispersal modes were assigned to 295 plant species. Animals dispersed the highest percentage of species (46.6%), while the percentage of autochorous and anemochorous species was 29.4 and 23%, respectively. The dispersal spectrum of the low forest-shrub vegetation type, based on the coverage of every species, showed that percentages of anemochorous (40.2%) and zoochorous species (37.8%) were similar. Autochory was the most important seed dispersal mode of the open-herbaceous vegetation (60%). Birds were the principal group of potential dispersers (58.9%) of zoochorous species, and reptiles the least important. Two marked fruiting peaks were found, one from the end of the dry season to the beginning of the wet season and the second one from the beginning to the middle of the dry season. The results showed that besides the differences in the vegetation structure and floristic composition between the sandstone plateaus and the adjacent tall forest, there also exist differences in the dispersal spectra and the fruiting rhythms.

Chapter 7 presents a participatory research approach on fruit availability and seed dispersal with the indigenous community Nonuya of Peña Roja. This approach proceeds in four stages initially with indigenous people as passive field guides progressing to active researchers of the project. The starting point was the distant relationship between scientific and indigenous peoples' knowledge. The first stage (the guide approach) consisted of the participation of indigenous people in a formal scientific research merely as guides, where there was little exchange of knowledge. During the second stage (the field-assistant approach) the guide became a field-assistant, and received training and expertise in scientific methodologies for data collection. In the third stage (from field-assistant to researcher), the indigenous field-assistant realised that it was necessary to know more about nature, his territory, culture, and myths. He proposed his "own research" where he successfully combined both scientific methodologies and dialogue with elders for obtaining information. In the last stage of the process (the researcher approach), information of high-quality and relevance to the needs of indigenous people was generated. In addition, the indigenous researcher learnt more about his own cultures' classification systems, traditions, stories and myths. The interaction between scientists and indigenous researchers allowed the exchange of experiences, methodologies and learnings, and provided tools for understanding ecological observations and/or cultural beliefs. As a result of this, and previous participatory approaches a direct a common knowledge dialogue between formal scientists and indigenous people has been established in this region of Colombian Amazonia.

The final chapter, the general discussion, proposes that the combination of the type of dispersal agent and the seed displacement will result in a particular seed shadow, which seems to explain the spatial distribution of common plant species of terra firme forests on the local scale. Additionally, it is proposed that seed dispersal processes in the Middle Caquetá region are limited both by the low fruit production and the low animal densities. The low fruit production in the vast terra firme forests of the Tertiary sedimentary plain, which is particularly notorious during certain year periods, is compensated by complementary fruiting phenologies in other ecosystems (*i.e.* sandstone plateaus), or group of plants such as climbers and epiphytes and/or cultivated fruiting trees. This complementarity, enhances seed dispersal of either ecosystem or plant-guilds, as competition for seed dispersers is minimised. Finally, I discuss about the working methodologies used in this research: observations at the canopy level were advantageous for recording fruiting patterns, frugivore activity and seed dispersal processes occurring at the highest levels of the forest. Participatory research stimulated dialogue and a common knowledge exchange between formal scientists and indigenous people, and facilitated dissemination of the results among local people.

Appendix 1. Floristic composition of the study site obtained during the BSc. thesis of Castaño-A. (2003) developed whithin the framework of this Ph.D. thesis. Density, frequency, dominance, diversity and Importance Value Index (IVI; Mueller-Dombois & Ellenberg 1974) of vascular plant species (DBH > 1 cm) sampled in sixteen widely distributed 50 x 2 m transects throughout a 64-ha area in a terra firme rain forest in Colombian Amazonia. N: number of individuals, * New records for the area.

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
ANACARDIACEAE	3	0.162		0.463	0.237	0.862
Tapirira guianensis Aubl.	3	0.162	0.295	0.463		0.919
ANNONACEAE	67	3.608		0.537	3.555	7.700
Anaxagorea aff. *phaeocarpa* Mart.	16	0.862	0.688	0.031		1.580
Annona NCA600	3	0.162	0.295	0.041		0.497
Bocageopsis canescens (Spruce ex Benth.) R.E.Fr.	1	0.054	0.098	0.001		0.153
Duguetia aff. *latifolia* R.E.Fr.	5	0.269	0.393	0.004		0.666
Duguetia NCA701	1	0.054	0.098	0.004		0.156
Guatteria recurvisepala R.E.Fr.	1	0.054	0.098	0.001		0.153
Guatteria stipitata R.E.Fr.	1	0.054	0.098	0.000		0.152
Guatteriella tomentosa Rusby	8	0.431	0.491	0.056		0.978
Guatteria NCA846	1	0.054	0.098	0.014		0.166
Oxandra euneura Diels	10	0.539	0.688	0.047		1.273
Unonopsis elegantissima R.E.Fr.	1	0.054	0.098	0.000		0.152
Unonopsis aff. *matthewsii* (Benth.) R.E.Fr.	1	0.054	0.098	0.002		0.154
Unonopsis stipitata Diels	14	0.754	0.884	0.039		1.677
Xylopia calophylla R.E.Fr.	1	0.054	0.098	0.281		0.433
Xylopia cuspidata Diels	3	0.162	0.295	0.016		0.472
APOCYNACEAE	25	1.346		0.679	2.370	4.394
Ambelania cf. *occidentalis* Zarucchi	2	0.108	0.196	0.002		0.306
Aspidosperma excelsum Benth.	6	0.323	0.196	0.012		0.532
Aspidosperma schultesii Woodson	3	0.162	0.196	0.094		0.452
Aspidosperma NCA1121	1	0.054	0.098	0.304		0.456
Aspidosperma NCA657	1	0.054	0.098	0.224		0.376
Lacmellea NCA371	5	0.269	0.393	0.020		0.682
Odontadenia verrucosa (Willd. ex Roem. & Schult.) K.Schum. ex Markgr.	1	0.054	0.098	0.000		0.152
Tabernaemontana disticha A.DC.	1	0.054	0.098	0.002		0.154
Tabernaemontana macrocalyx Müll. Arg.	4	0.215	0.196	0.009		0.421
Tabernaemontana NCA872	1	0.054	0.098	0.012		0.164
ARACEAE	4	0.215		0.010	0.711	0.936
* *Heteropsis tenuispadix* G.S. Bunting	1	0.054	0.098	0.003		0.155
Philodendron megalophyllum Schott	1	0.054	0.098	0.003		0.155
* *Philodendron steyermarkii* G.S. Bunting	2	0.108	0.196	0.004		0.308
ARALIACEAE	3	0.162		0.066	0.237	0.464
Dendropanax arboreus (L.) Decne. & Planch.	3	0.162	0.098	0.066		0.326
ARECACEAE	278	14.970		1.454	2.844	19.268
Attalea racemosa Spruce	15	0.808	1.081	0.263		2.151
Bactris acanthocarpa Mart. var. *exscapa* Barb. Rodr.	1	0.054	0.098	0.002		0.154
Bactris fissifrons Mart.	6	0.323	0.393	0.007		0.723
Bactris hirta Mart.	1	0.054	0.098	0.001		0.153
Bactris maraja Mart.	1	0.054	0.098	0.001		0.153
Geonoma maxima (Poit.) Kunth	15	0.808	0.393	0.105		1.305
Iriartella setigera (Mart.) H. Wendl.	22	1.185	0.786	0.030		2.000
Lepidocaryum tenue Mart.	153	8.239	1.375	0.634		10.244
Oenocarpus bataua Mart.	45	2.423	1.473	0.139		4.034
Oenocarpus minor Mart.	7	0.377	0.589	0.195		1.161
Pholidostachys synanthera (Mart.) H. E. Moore	10	0.539	0.098	0.056		0.692

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
Socratea exorrhiza (Mart.) H. Wendl.	2	0.108	0.196	0.022		0.326
BIGNONIACEAE	14	0.754		0.110	1.422	2.286
Arrabidaea corallina (Jacq.) Sandwith	2	0.108	0.196	0.008		0.312
Arrabidaea NCA1131	1	0.054	0.098	0.001		0.153
Distictis cf. *granulosa* (Klotzsch) Bureau & K.Schum.	1	0.054	0.098	0.008		0.160
Jacaranda cf. *macrocarpa* Bureau & K.Schum.	8	0.431	0.491	0.091		1.012
Pleonotoma melioides (S. Moore) A.H. Gentry	1	0.054	0.098	0.001		0.153
Bignoniaceae indeterminada	1	0.054	0.098	0.002		0.154
BOMBACACEAE	7	0.377		0.271	0.237	0.885
Scleronema micranthum (Ducke) Ducke	7	0.377	0.491	0.271		1.139
BURSERACEAE	100	5.385		5.057	3.318	13.760
Crepidospermum cf. *rhoifolium* (Benth.) Triana & Planch.	5	0.269	0.196	0.006		0.472
Dacryodes chimantensis Steyerm. & Maguire	20	1.077	0.884	0.109		2.070
Protium altsonii Sandwith	1	0.054	0.098	0.001		0.153
* *Protium angustifolium* Swart	2	0.108	0.098	0.209		0.415
Protium aff. *angustifolium* Swart	3	0.162	0.196	0.054		0.412
Protium apiculatum Swart	5	0.269	0.295	0.009		0.573
Protium aracouchini (Aubl.) Marchand	4	0.215	0.295	0.011		0.521
Protium crassipetalum Cuatrec.	39	2.100	1.081	0.312		3.491
Protium cf. *decandrum* (Aubl.) Marchand	4	0.215	0.295	4.314		4.824
Protium divaricatum Engl.	1	0.054	0.098	0.001		0.153
Protium opacum Swart	1	0.054	0.098	0.001		0.153
Protium paniculatum Engl.	12	0.646	0.589	0.026		1.261
Protium spruceanum (Benth.) Engl.	2	0.108	0.196	0.003		0.307
Protium aff. *trifoliolatum* Engl.	1	0.054	0.098	0.003		0.155
CAESALPINIACEAE	24	1.292		0.777	1.659	3.728
Bauhinia cf. *guianensis* Aubl.	2	0.108	0.196	0.033		0.337
Cynometra cf. *marginata* Benth.	1	0.054	0.098	0.003		0.155
Tachigali formicarum Harms	4	0.215	0.196	0.005		0.417
Tachigali cf. *paniculata* Aubl.	2	0.108	0.196	0.063		0.367
Tachigali cf. *polyphylla* Poepp.	9	0.485	0.786	0.184		1.454
Tachigali NCA1353	1	0.054	0.098	0.458		0.610
Tachigali NCA880	5	0.269	0.295	0.032		0.596
CAPPARACEAE	1	0.054		0.007	0.237	0.298
Capparis detonsa Triana & Planch.	1	0.054	0.098	0.007		0.159
CARYOCARACEAE	1	0.054		0.052	0.237	0.343
* *Anthodiscus* cf. *obovatus* Benth. ex Wittm.	1	0.054	0.098	0.052		0.204
CECROPIACEAE	3	0.162		0.003	0.474	0.639
Pourouma formicarum Ducke	1	0.054	0.098	0.002		0.154
Pourouma myrmecophila Ducke	2	0.108	0.196	0.001		0.305
CHRYSOBALANACEAE	34	1.831		1.013	3.791	6.635
Couepia canomensis (Mart.) Benth. ex Hook.f.	1	0.054	0.098	0.578		0.730
Couepia chrysocalyx (Poepp. & Endl.) Benth. ex Hook.f.	7	0.377	0.589	0.068		1.034
* *Couepia* cf. *edulis* (Prance) Prance	2	0.108	0.196	0.202		0.506
Couepia trapezioana Cuatrec.	1	0.054	0.098	0.012		0.164
* *Hirtella americana* L.	5	0.269	0.295	0.005		0.569
Hirtella aff. *rodriguesii* Prance	2	0.108	0.196	0.094		0.398
Hirtella NCA921	2	0.108	0.098	0.004		0.209
Hirtella NCA966	1	0.054	0.098	0.008		0.160
Licania granvillei Prance	1	0.054	0.098	0.009		0.161
Licania aff. *heteromorpha* (C. Mart.ex Hoof. f.) Benth.	2	0.108	0.196	0.003		0.307
Licania cf. *lata* J. F. Macbr.	4	0.215	0.295	0.019		0.529
Licania reticulata Prance	2	0.108	0.098	0.003		0.209

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
Licania triandra Mart. ex Hook. f.	1	0.054	0.098	0.001		0.153
Licania vaupesiana Killip & Cuatrec.	1	0.054	0.098	0.001		0.153
Licania NCA569	1	0.054	0.098	0.003		0.155
Licania NCA434	1	0.054	0.098	0.004		0.156
CLUSIACEAE	50	2.693		0.828	4.502	8.023
Calophyllum NCA949	1	0.054	0.098	0.213		0.365
Chrysochlamys cf. *laxa* Planch. & Triana	1	0.054	0.098	0.003		0.155
Chrysochlamys weberbaueri Engl.	2	0.108	0.196	0.005		0.309
Clusia cf. *cruciata* Cuatrec.	1	0.054	0.098	0.005		0.157
Clusia gaudichaudii Choisy	1	0.054	0.098	0.003		0.155
Clusia grammadenioides Pipoly	15	0.808	0.786	0.095		1.689
Clusia cf. *minor* L.	3	0.162	0.196	0.042		0.400
Clusia aff. *microstemon* Planch. & Triana	1	0.054	0.098	0.001		0.153
Clusia viscida Engl.	1	0.054	0.098	0.001		0.153
Clusia NCA950	2	0.108	0.098	0.014		0.220
Havetiopsis aff. *flexilis* Spruce ex Planch. & Triana	4	0.215	0.295	0.095		0.605
* *Platonia insignis* Mart.	1	0.054	0.098	0.013		0.165
Tovomita brasilensis (Mart.) Walp.	1	0.054	0.098	0.001		0.153
Tovomita aff. *pyrifolia* Planch. & Triana	2	0.108	0.196	0.019		0.323
Tovomita schomburgkii Planch. & Triana	4	0.215	0.393	0.077		0.685
Tovomita spruceana Planch. & Triana	2	0.108	0.196	0.055		0.359
Tovomita NCA473	1	0.054	0.098	0.001		0.153
Vismia cf. *cayennensis* (Jacq.) Pers.	2	0.108	0.196	0.006		0.310
NCA730	5	0.269	0.393	0.180		0.842
COMBRETACEAE	2	0.108		1.777	0.474	2.358
Buchenavia amazonica Alwan & Stace	1	0.054	0.098	1.767		1.919
Buchenavia cf. *macrophylla* Eichler	1	0.054	0.098	0.009		0.161
CONNARACEAE	7	0.377		0.038	0.711	1.126
Connarus faciculatus (DC.) Planch.	1	0.054	0.098	0.001		0.153
Pseudoconnarus macrophyllus (Poepp.) Radlk.	5	0.269	0.295	0.037		0.601
Pseudoconnarus rhynchosioides (Standl.) Prance	1	0.054	0.098	0.001		0.153
CONVOLVULACEAE	10	0.539		0.043	1.659	2.240
Dicranostyles ampla Ducke	3	0.162	0.295	0.022		0.478
Dicranostyles holostyla Ducke	2	0.108	0.196	0.002		0.306
Dicranostyles laxa Ducke	1	0.054	0.098	0.001		0.153
Dicranostyles cf. *scandens* Benth.	1	0.054	0.098	0.001		0.153
Dicranostyles sericea Gleason	1	0.054	0.098	0.004		0.156
Dicranostyles NCA945	1	0.054	0.098	0.008		0.160
Maripa cf. *glabra* Choisy	1	0.054	0.098	0.005		0.157
CUCURBITACEAE	2	0.108		0.003	0.237	0.348
Fevillea NCA433	2	0.108	0.196	0.003		0.307
CYATHEACEAE	2	0.108		0.011	0.237	0.356
Cyathea NCA723	2	0.108	0.196	0.011		0.315
DILLENIACEAE	8	0.431		0.015	0.711	1.157
Doliocarpus dentatus (Aubl.) Standl.	5	0.269	0.295	0.009		0.573
Doliocarpus NCA490	1	0.054	0.098	0.004		0.156
Pinzona coriacea Mart. & Zucc.	2	0.108	0.196	0.001		0.306
DIPTEROCARPACEAE	33	1.777		14.525	0.237	16.539
Pseudomonotes tropenbosii A.C. Londoño, E. Alvarez & Forero	33	1.777	1.179	14.525		17.480
EBENACEAE	2	0.108		0.005	0.474	0.587
* *Diospyros bullata* A. C. Sm.	1	0.054	0.098	0.003		0.155
Diospyros glomerata Spruce	1	0.054	0.098	0.002		0.154
ELAEOCARPACEAE	9	0.485		0.870	1.422	2.776
Sloanea floribunda Spruce ex Benth.	2	0.108	0.196	0.193		0.497
Sloanea guianensis (Aubl.) Benth.	1	0.054	0.098	0.001		0.153
Sloanea aff. *guianensis* (Aubl.) Benth.	1	0.054	0.098	0.001		0.153

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
Sloanea cf. *laxiflora* Spruce ex Benth.	1	0.054	0.098	0.008		0.160
Sloanea aff. *robusta* Uittien	3	0.162	0.196	0.393		0.750
Sloanea NCA1128	1	0.054	0.098	0.275		0.427
ERICACEAE	7	0.377		1.405	0.237	2.019
Satyria panurensis (Benth. ex Meisn.) Benth. & Hook. f. ex Nied.	7	0.377	0.688	1.405		2.470
EUPHORBIACEAE	71	3.823		1.208	1.896	6.927
Hevea pauciflora (Spruce ex Benth.) Müll.Arg.	5	0.269	0.196	0.077		0.543
Hevea NCA1004	4	0.215	0.393	0.166		0.774
Mabea NCA655	7	0.377	0.491	0.050		0.918
Micrandra spruceana (Baill.) R. E. Schult.	6	0.323	0.393	0.279		0.995
Pera NCA1360	1	0.054	0.098	0.171		0.323
Richeria grandis Vahl	5	0.269	0.393	0.021		0.683
Senefeldera aff. *verticillata* (Vell.) Croizat	25	1.346	0.688	0.381		2.414
Senefeldera NCA671	18	0.969	0.491	0.063		1.523
FABACEAE	92	4.954		18.324	6.872	30.037
Clathrotropis macrocarpa Ducke	24	1.292	0.884	0.440		2.616
Dalbergia riedelii (Benth.) Sandwith	1	0.054	0.098	1.848		2.000
Derris NCA381	1	0.054	0.098	0.004		0.156
Diplotropis duckei Yakovlev	2	0.108	0.196	0.177		0.481
Diplotropis aff. *martiusii* Benth.	1	0.054	0.098	0.022		0.174
Diplotropis martiusii Benth.	3	0.162	0.196	0.029		0.387
* *Dipteryx punctata* (S.F. Blake) Amshoff	1	0.054	0.098	0.005		0.157
Hymenolobium pulcherrimum Ducke	1	0.054	0.098	0.013		0.165
Lonchocarpus nicou (Aubl.) DC.	7	0.377	0.589	0.021		0.987
Machaerium cf. *acutifolium* Vogel	1	0.054	0.098	0.001		0.153
Machaerium macrophyllum Benth.	10	0.539	0.589	0.017		1.145
Monopteryx uaucu Spruce ex Benth.	4	0.215	0.098	15.154		15.468
Myroxylon NCA408	1	0.054	0.098	0.001		0.153
Ormosia amazonica Ducke	3	0.162	0.295	0.005		0.461
Ormosia costulata (Miq.) Kleinhoonte	2	0.108	0.196	0.426		0.730
* *Platymiscium* cf. *pinnatum* (Jacq.) Dugand	1	0.054	0.098	0.002		0.154
Pterocarpus cf. *officinalis* Jacq.	5	0.269	0.393	0.039		0.701
Pterocarpus sp.	1	0.054	0.098	0.001		0.153
Swartzia benthamiana Miq.	1	0.054	0.098	0.044		0.196
* *Swartzia laurifolia* Benth.	1	0.054	0.098	0.032		0.184
Swartzia racemosa Benth.	1	0.054	0.098	0.013		0.165
Swartzia schomburgkii Benth.	2	0.108	0.196	0.003		0.307
Swartzia NCA778	2	0.108	0.196	0.001		0.305
Swartzia NCA632	3	0.162	0.196	0.003		0.361
Swartzia NCA871	1	0.054	0.098	0.002		0.154
Swartzia NCA439	3	0.162	0.098	0.006		0.266
Swartzia NCA662	1	0.054	0.098	0.001		0.153
Swartzia NCA378	5	0.269	0.393	0.007		0.669
Zygia basijuga (Ducke) Barneby & J.W. Grimes	2	0.108	0.196	0.006		0.310
NCA700	1	0.054	0.098	0.002		0.154
FLACOURTIACEAE	9	0.485		0.019	0.711	1.215
Carpotroche amazonica Mart. ex Eichler	2	0.108	0.196	0.001		0.306
Carpotroche NCA596	1	0.054	0.098	0.004		0.156
Ryania angustifolia (Turez.) Monach.	6	0.323	0.295	0.013		0.631
HELICONIACEAE	3	0.162		0.001	0.237	0.400
Heliconia lasiorachis L. Anderss.	3	0.162	0.196	0.001		0.359
HIPPOCRATEACEAE	3	0.162		0.005	0.474	0.640
Salacia bullata Mennega	1	0.054	0.098	0.001		0.153
Tontalea cf. *coriacea* A.C.Sm.	2	0.108	0.196	0.004		0.308
HUMIRIACEAE	6	0.323		0.080	0.237	0.640
Vantanea peruviana J.F. Macbr.	6	0.323	0.491	0.080		0.894

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
LACISTEMATACEAE	2	0.108		0.004	0.237	0.349
Lacistema aggregatum (P.J.Bergius) Rusby	2	0.108	0.196	0.004		0.308
LAURACEAE	72	3.877		1.311	5.687	10.876
Aiouea cf. *impressa* (Meisn.) Kosterm.	1	0.054	0.098	0.000		0.152
Anaueria NCA623	1	0.054	0.098	0.001		0.153
Aniba aff. *affinis* (Meisn.) Mez	5	0.269	0.295	0.123		0.687
Aniba hostmanniana (Nees) Mez	7	0.377	0.393	0.471		1.240
Beilschmiedia aff. *curviramea* (Meisn.) Kosterm.	1	0.054	0.098	0.101		0.253
Endlicheria aff. *formosa* A. C. Sm.	1	0.054	0.098	0.004		0.156
Endlicheria cf. *gracilis* Kosterm.	6	0.323	0.295	0.006		0.624
Endlicheria pyriformis (Nees) Mez	4	0.215	0.295	0.016		0.526
Endlicheria NCA493	1	0.054	0.098	0.007		0.159
Licaria cf. *guianensis* Aubl.	1	0.054	0.098	0.006		0.158
Nectandra umbrosa (Kunth) Mez	1	0.054	0.098	0.000		0.152
Nectandra NCA855	2	0.108	0.196	0.002		0.306
Ocotea aciphylla (Ness) Mez	3	0.162	0.295	0.034		0.490
Ocotea amazonica (Meisn.) Mez	2	0.108	0.098	0.003		0.208
Ocotea argyrophylla Ducke	8	0.431	0.491	0.032		0.954
Ocotea aff. *cernua* (Nees) Mez	2	0.108	0.196	0.005		0.309
Ocotea aff. *javitensis* (Kunth) Pittier	6	0.323	0.295	0.006		0.624
Ocotea longifolia Kunth	13	0.700	0.589	0.088		1.377
Ocotea martiniana (Nees) Mez	1	0.054	0.098	0.002		0.154
Ocotea aff. *petalanthera* (Meisn.) Mez	1	0.054	0.098	0.344		0.496
Persea NCA747	1	0.054	0.098	0.001		0.153
Pleurothyrium vasquezii van der Werff	1	0.054	0.098	0.002		0.154
Rhodostemonodaphne cf. *negrensis* Madriñán	2	0.108	0.196	0.053		0.357
Rhodostemonodaphne NCA777	1	0.054	0.098	0.002		0.154
LECYTHIDACEAE	150	8.078		10.986	5.450	24.513
Cariniana decandra Ducke	5	0.269	0.393	0.026		0.688
Cariniana NCA619	1	0.054	0.098	0.006		0.158
Couratari cf. *stellata* A.C.Sm.	1	0.054	0.098	0.041		0.194
Eschweilera alata A. C. Sm.	3	0.162	0.295	0.014		0.470
Eschweilera albiflora (DC.) Miers	21	1.131	0.786	1.534		3.450
Eschweilera andina (Rusby) J.F.Macbr.	11	0.592	0.491	0.077		1.160
Eschweilera bracteosa (Poepp. ex Berg) Miers	19	1.023	0.688	0.343		2.053
Eschweilera coriacea (DC.) S. A. Mori	8	0.431	0.688	0.332		1.450
Eschweilera cf. *decolorans* Sandwith	2	0.108	0.098	0.007		0.213
Eschweilera gigantea (R. Knuth) J.F.Macbr.	10	0.539	0.295	0.132		0.965
Eschweilera laevicarpa S.A. Mori	3	0.162	0.196	0.010		0.368
Eschweilera parvifolia Mart. ex DC.	12	0.646	0.688	0.512		1.846
Eschweilera cf. *pedicellata* (Rich.) S. A. Mori	3	0.162	0.196	0.011		0.369
Eschweilera punctata S. A. Mori	10	0.539	0.589	6.709		7.836
Eschweilera aff. *rufifolia* S.A. Mori	1	0.054	0.098	0.021		0.173
Eschweilera tessmannii R. Knuth	6	0.323	0.393	0.051		0.767
Eschweilera NCA627	11	0.592	0.688	0.193		1.473
Eschweilera NCA759	2	0.108	0.196	0.007		0.311
Eschweilera NCA1061	5	0.269	0.295	0.672		1.236
Eschweilera NCA838	1	0.054	0.098	0.123		0.275
Eschweilera NCA415	11	0.592	0.295	0.090		0.976
Lecythis cf. *chartacea* O. Berg	3	0.162	0.295	0.005		0.461
Lecythis pisonis Cambess.	1	0.054	0.098	0.069		0.221
LINACEAE	5	0.269		0.007	0.474	0.750
Roucheria calophylla Planch.	1	0.054	0.098	0.001		0.153
Roucheria punctata (Ducke) Ducke	4	0.215	0.295	0.006		0.516
LOGANIACEAE	2	0.108		0.002	0.237	0.347
Strychnos solerederi Gilg	2	0.108	0.196	0.002		0.306

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
LORANTHACEAE	2	0.108		0.005	0.237	0.350
Phthirusa retroflexa (Ruiz & Pav.) Kuijt	2	0.108	0.196	0.005		0.309
MALPIGHIACEAE	4	0.215		0.037	0.711	0.964
Banisteriopsis NCA451	1	0.054	0.098	0.001		0.153
* *Diplopterys cabrerana* (Cuatrec.) B. Gates	2	0.108	0.196	0.027		0.331
MARANTACEAE	3	0.162		0.002	0.474	0.638
Calathea altissima (Poepp. & Endl.) Körn.	2	0.108	0.196	0.002		0.306
Ischnosiphon puberulus Loes.	1	0.054	0.098	0.001		0.153
MARCGRAVIACEAE	1	0.054		0.003	0.237	0.294
Marcgravia cf. *eichleriana* Wittm.	1	0.054	0.098	0.003		0.155
MELASTOMATACEAE	33	1.777		0.227	3.791	5.796
* *Adelobotrys* cf. *adscendens* (Sw.) Triana	3	0.162	0.295	0.004		0.460
Clidemia bernardii Wurdack	5	0.269	0.393	0.004		0.666
* *Graffenrieda miconioides* Naudin	1	0.054	0.098	0.005		0.157
Miconia cf. *calvescens* DC.	2	0.108	0.196	0.007		0.311
Miconia eugenioides Triana	5	0.269	0.295	0.084		0.647
Miconia cf. *lamprophylla* Triana	1	0.054	0.098	0.059		0.211
Miconia cf. *lepidota* Schrank & Mart.ex DC.	4	0.215	0.295	0.023		0.533
Miconia cf. *longifolia* (Aubl.) DC.	2	0.108	0.196	0.002		0.306
Miconia phanerostila Pilg.	2	0.108	0.196	0.001		0.305
Miconia cf. *prasina* (Sw.) DC.	1	0.054	0.098	0.004		0.156
Miconia aff. *spichigera* Wurdack	1	0.054	0.098	0.001		0.153
Miconia cf. *splendens* (Sw.) Griseb.	2	0.108	0.196	0.023		0.327
Miconia tomentosa (Rich.) D.Don ex DC.	1	0.054	0.098	0.009		0.161
Miconia NCA361	1	0.054	0.098	0.001		0.153
Mouriri cauliflora Mart. ex DC.	1	0.054	0.098	0.001		0.153
Mouriri cf. *myrtifolia* Spruce ex Triana	1	0.054	0.098	0.001		0.153
MELIACEAE	23	1.239		0.152	2.370	3.760
* *Guarea ecuadoriensis* W. Palacios	1	0.054	0.098	0.009		0.161
Guarea guidonia (L.) Sleumer	6	0.323	0.295	0.067		0.684
Guarea aff. *kunthiana* A. Juss.	1	0.054	0.098	0.008		0.160
Guarea macrophylla Vahl	2	0.108	0.196	0.016		0.320
Guarea pubescens (Rich.) A. Juss.	1	0.054	0.098	0.001		0.153
Guarea silvatica C. DC.	3	0.162	0.295	0.008		0.464
Guarea trunciflora C. DC.	1	0.054	0.098	0.008		0.160
Trichilia cf. *micrantha* Benth.	4	0.215	0.393	0.021		0.629
Trichilia cf. *pleeana* (A. Juss.) C. DC.	2	0.108	0.196	0.003		0.307
Trichilia poeppigii C. DC.	2	0.108	0.196	0.010		0.314
MENISPERMACEAE	15	0.808		0.069	1.185	2.062
Abuta imene (Mart.) Eichler	3	0.162	0.098	0.006		0.266
Abuta NCA620	2	0.108	0.196	0.001		0.305
Telitoxicum aff. *krukovii* Moldenke	3	0.162	0.196	0.028		0.386
Telitoxicum NCA915	2	0.108	0.196	0.009		0.313
MENDONCIACEAE	2	0.108		0.003	0.237	0.348
Mendoncia coccinea Vell.	2	0.108	0.098	0.003		0.209
MIMOSACEAE	188	10.124		21.246	2.844	34.328
Abarema leucophylla (Spruce ex Benth.) Barneby & J.W. Grimes	4	0.215	0.295	0.125		0.635
Abarema NCA414	13	0.700	0.295	0.102		1.097
Inga pruriens Poepp.	1	0.054	0.098	0.001		0.153
Inga tessmannii Harms	2	0.108	0.196	0.002		0.306
Inga NCA507	9	0.485	0.589	0.021		1.095
Inga NCA588	2	0.108	0.098	0.009		0.215
Parkia igneiflora Ducke	1	0.054	0.098	0.008		0.160
Parkia panurensis Benth. ex H.C. Hopkins	1	0.054	0.098	0.073		0.225
Parkia NCA542	4	0.215	0.393	19.908		20.517
NCA1238	150	8.078	1.081	0.012		9.165

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
NCA834	1	0.054	0.098	0.986		1.138
MONIMIACEAE	3	0.162		0.006	0.711	0.879
Mollinedia NCA873	1	0.054	0.098	0.001		0.153
Siparuna aff. *guianensis* Aubl.	1	0.054	0.098	0.005		0.157
Siparuna cf. *monogyna* Jangoux	1	0.054	0.098	0.001		0.153
MORACEAE	51	2.746		6.111	2.607	11.464
Brosimum longifolium Ducke	1	0.054	0.098	0.044		0.196
Brosimum rubescens Taub.	22	1.185	0.982	2.151		4.318
Brosimum utile (Kunth.) Pittier	9	0.485	0.589	2.119		3.192
Helicostylis scabra (J.F. Macbr.) C.C. Berg	1	0.054	0.098	0.000		0.152
Helicostylis tomentosa (Poepp. & Endl.) Rusby	1	0.054	0.098	0.005		0.157
Pseudolmedia laevigata Trécul	5	0.269	0.393	1.470		2.132
Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.	2	0.108	0.196	0.292		0.596
Pseudolmedia rigida (Klotzsch & H.Karst.) Cuatrec.	1	0.054	0.098	0.001		0.153
Sorocea muriculata Miq.	3	0.162	0.295	0.007		0.464
Sorocea pubivena Hemsl.	3	0.162	0.196	0.005		0.363
Trymatococcus amazonicus Poepp. & Endl.	3	0.162	0.196	0.017		0.375
MYRISTICACEAE	114	6.139		1.494	4.028	11.661
Compsoneura capitellata (A. DC.) Warb.	8	0.431	0.295	0.074		0.799
Compsoneura sprucei (A. DC.) Warb.	2	0.108	0.196	0.176		0.480
Compsoneura NCA455	1	0.054	0.098	0.001		0.153
Iryanthera crassifolia A.C.Sm.	1	0.054	0.098	0.001		0.153
Iryanthera juruensis Warb.	1	0.054	0.098	0.001		0.153
Iryanthera laevis Markgr.	4	0.215	0.295	0.171		0.681
Iryanthera lancifolia Ducke	11	0.592	0.393	0.215		1.200
Iryanthera polyneura Ducke	14	0.754	0.589	0.031		1.374
Iryanthera tricornis Ducke	1	0.054	0.098	0.008		0.160
Iryanthera ulei Warb.	31	1.669	0.982	0.387		3.038
Virola calophylla (Spruce) Warb.	6	0.323	0.295	0.124		0.742
Virola carinata (Benth.) Warb.	1	0.054	0.098	0.138		0.290
Virola elongata (Benth.) Warb.	2	0.108	0.196	0.011		0.315
Virola obovata Ducke	13	0.700	0.393	0.105		1.198
Virola pavonis (A.DC.) A.C.Sm.	7	0.377	0.589	0.008		0.974
* *Virola venosa* (Benth.) Warb.	10	0.539	0.589	0.042		1.170
Virola NCA1381	1	0.054	0.098	0.002		0.154
MYRSINACEAE	3	0.162		0.006	0.474	0.642
Cybianthus guianensis (A.DC.) Miq.	2	0.108	0.098	0.006		0.212
Cybianthus cf. *longifolius* Miq.	1	0.054	0.098	0.001		0.153
MYRTACEAE	5	0.269		0.018	0.948	1.235
Eugenia NCA377	1	0.054	0.098	0.001		0.153
Marlierea caudata Mc Vaugh	1	0.054	0.098	0.006		0.158
Myrcia cf. *splendens* (Sw.) DC.	2	0.108	0.196	0.011		0.315
NCA1417	1	0.054	0.098	0.001		0.153
NYCTAGINACEAE	10	0.539		0.024	1.659	2.222
Neea divaricata Poepp. & Endl.	1	0.054	0.098	0.004		0.156
Neea macrophylla Poepp. & Endl.	1	0.054	0.098	0.002		0.154
Neea parviflora Poepp. & Endl.	1	0.054	0.098	0.003		0.155
Neea verticillata Ruiz & Pav.	3	0.162	0.196	0.005		0.363
Neea NCA311	1	0.054	0.098	0.004		0.156
Neea NCA457	2	0.108	0.098	0.004		0.210
Pisonia NCA1214	1	0.054	0.098	0.003		0.155
OCHNACEAE	5	0.269		0.015	0.711	0.995
Ouratea pendula Poepp. ex Engl.	1	0.054	0.098	0.001		0.153
Ouratea weberbaueri Sleumer	2	0.108	0.196	0.009		0.313
Ouratea aff. *weberbaueri* Sleumer	2	0.108	0.196	0.004		0.308

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
OLACACEAE	6	0.323		0.028	0.711	1.062
Dulacia macrophylla (Benth.) Kuntze	1	0.054	0.098	0.001		0.153
Heisteria duckei Sleumer	4	0.215	0.393	0.027		0.635
Minquartia guianensis Aubl.	1	0.054	0.098	0.001		0.153
PASSIFLORACEAE	1	0.054		0.001	0.237	0.291
Dilkea parviflora Killip	1	0.054	0.098	0.001		0.153
PIPERACEAE	3	0.162		0.011	0.474	0.647
Piper arboreum Aubl.	2	0.108	0.196	0.010		0.314
Piper poporense Trel. & Yunck.	1	0.054	0.098	0.001		0.153
POLYGALACEAE	8	0.431		0.029	0.711	1.171
Moutabea cf. *guianensis* Aubl.	5	0.269	0.393	0.007		0.669
Moutabea longifolia Poepp. & Endl.	1	0.054	0.098	0.001		0.153
Moutabea NCA742	2	0.108	0.196	0.022		0.326
POLYGONACEAE	6	0.323		0.012	0.474	0.809
* *Coccoloba polystachya* Wedd.	5	0.269	0.196	0.011		0.477
Triplaris NCA711	1	0.054	0.098	0.001		0.153
QUIINACEAE	5	0.269		0.007	0.474	0.750
Quiina cf. *leptoclada* Tul.	1	0.054	0.098	0.001		0.153
Quiina longifolia Spruce ex Planch. & Triana	4	0.215	0.196	0.006		0.418
RHAMNACEAE	37	1.992		0.262	0.237	2.491
Ampelozizyphus amazonicus Ducke	37	1.992	0.982	0.262		3.235
RHIZOPHORACEAE	10	0.539		0.391	0.474	1.403
Sterigmapetalum obovatum Kuhlm.	5	0.269	0.295	0.317		0.881
Sterigmapetalum NCA630	5	0.269	0.393	0.073		0.736
RUBIACEAE	44	2.369		0.267	4.976	7.612
Amaioua cf. *corymbosa* Kunth.	1	0.054	0.098	0.002		0.154
* *Borojoa claviflora* (K. Schum.) Cuatrec.	4	0.215	0.393	0.032		0.640
Botryarrhena pendula Ducke	1	0.054	0.098	0.003		0.155
Coussarea cf. *bernardii* Steyerm.	2	0.108	0.196	0.003		0.307
Coussarea aff. *durifolia* Dwyer	1	0.054	0.098	0.002		0.154
* *Coussarea violacea* Aubl.	1	0.054	0.098	0.097		0.249
Duroia saccifera (Mart.ex Roem. & Schult.) Hook.f. ex Schumann.	4	0.215	0.393	0.019		0.627
Faramea capillipes Müll.Arg.	1	0.054	0.098	0.002		0.154
Faramea NCA976	2	0.108	0.196	0.001		0.306
Genipa americana L.	1	0.054	0.098	0.000		0.152
Pagamea macrophylla Spruce ex Benth.	3	0.162	0.196	0.022		0.380
Palicourea cf. *anisoloba* (Müll.Arg.) B.M.Boom. & M.T.Campos	1	0.054	0.098	0.002		0.154
Palicourea corymbifera (Müll.Arg.) Standl.	4	0.215	0.295	0.005		0.515
* *Psychotria huampamiensis* C. M. Taylor	2	0.108	0.196	0.003		0.307
Psychotria poeppigiana Müll.Arg.	1	0.054	0.098	0.001		0.153
Psychotria NCA517	6	0.323	0.196	0.049		0.568
Psychotria NCA342	1	0.054	0.098	0.002		0.154
Psychotria NCA884	2	0.108	0.196	0.002		0.306
Rudgea duidae (Standl.) Steyerm.	4	0.215	0.295	0.007		0.517
NCA1100	1	0.054	0.098	0.007		0.159
NCA1089	1	0.054	0.098	0.007		0.159
SABIACEAE	7	0.377		0.123	0.474	0.974
Meliosma NCA699	2	0.108	0.196	0.080		0.384
Ophiocaryum heterophyllum (Benth.) Urb.	5	0.269	0.393	0.043		0.705
SAPINDACEAE	12	0.646		0.053	1.896	2.595
* *Matayba* cf. *adenanthera* Radlk.	1	0.054	0.098	0.004		0.156
Matayba aff. *arborescens* (Aubl.) Radlk.	1	0.054	0.098	0.000		0.152
Paullinia cf. *capreolata* (Aubl.) Radlk.	2	0.108	0.196	0.008		0.312
Talisia carinata Radlk.	1	0.054	0.098	0.005		0.157
Talisia cerasina (Benth.) Radlk.	2	0.108	0.196	0.003		0.307

Plant species	N	Relative density	Relative frequency	Relative dominance	Relative diversity	IVI
Talisia clathrata Radlk.	2	0.108	0.196	0.021		0.325
Talisia mollis Cambess.	1	0.054	0.098	0.001		0.153
Talisia NCA573	2	0.108	0.196	0.012		0.316
SAPOTACEAE	84	4.523		2.083	7.583	14.189
Chrysophyllum aff. *amazonicum* T.D.Penn.	2	0.108	0.196	0.072		0.376
Chrysophyllum colombianum (Aubrév.) T.D.Penn.	1	0.054	0.098	0.002		0.154
Chrysophyllum sanguinolentum (Pierre) Baehni	9	0.485	0.589	0.495		1.569
Chrysophyllum superbum T.D.Penn.	1	0.054	0.098	0.003		0.155
Ecclinusa lanceolata (Mart. & Eichler) Pierre	2	0.108	0.196	0.037		0.341
Elaeoluma cf. glabrescens (Mart. & Eichl.) Aubrév.	1	0.054	0.098	0.001		0.153
Manilkara bidentata (A.DC.) A.Chev.	1	0.054	0.098	0.199		0.351
Manilkara inundata (Ducke) Ducke	1	0.054	0.098	0.005		0.157
Micropholis cf. *casiquiarensis* Aubrév.	1	0.054	0.098	0.003		0.155
Micropholis egensis (A.DC.) Pierre	3	0.162	0.196	0.396		0.754
Micropholis madeirensis (Baehni) Aubrév.	2	0.108	0.196	0.130		0.434
Micropholis melinoniana Pierre	4	0.215	0.393	0.032		0.640
Micropholis NCA458	6	0.323	0.393	0.012		0.728
Pouteria baehniana Monach.	1	0.054	0.098	0.304		0.456
Pouteria bangii (Rusby) T.D. Penn.	2	0.108	0.196	0.003		0.307
Pouteria caimito (Ruiz & Pav.) Radlk.	3	0.162	0.196	0.015		0.373
Pouteria cladantha Sandwith	1	0.054	0.098	0.001		0.153
Pouteria cuspidata (A.DC.) Baehni	1	0.054	0.098	0.046		0.199
Pouteria aff. *glauca* T.D.Penn.	1	0.054	0.098	0.000		0.152
Pouteria guianensis Aubl.	10	0.539	0.589	0.028		1.156
Pouteria maguirei (Aubrév.) T.D.Penn.	3	0.162	0.295	0.031		0.487
* *Pouteria plicata* T.D.Penn.	2	0.108	0.098	0.051		0.257
Pouteria reticulata (Engl.) Eyma	2	0.108	0.196	0.003		0.307
Pouteria aff. *rostrata* (Huber) Baehni	1	0.054	0.098	0.003		0.155
Pouteria torta (Mart.) Radlk.	2	0.108	0.196	0.001		0.306
Pouteria aff. *trilocularis* Cronquist	2	0.108	0.196	0.003		0.307
Pouteria ucuqui Pires & R.E.Schult.	3	0.162	0.295	0.136		0.592
Pouteria venosa (Mart.) Baehni	4	0.215	0.295	0.019		0.529
Pouteria williamii (Aubrév. & Pellegr.) T.D.Penn.	2	0.108	0.196	0.017		0.321
Pouteria NCA320	3	0.162	0.295	0.021		0.478
Pouteria NCA954	1	0.054	0.098	0.003		0.155
Pouteria NCA848	6	0.323	0.295	0.010		0.628
STERCULIACEAE	4	0.215		0.002	0.474	0.692
* *Sterculia pendula* Ducke	1	0.054	0.098	0.000		0.152
Theobroma subincanum Mart.	3	0.162	0.196	0.002		0.360
TILIACEAE	1	0.054		0.001	0.237	0.291
Apeiba aspera Aubl.	1	0.054	0.098	0.001		0.153
TRIGONACEAE	1	0.054		0.006	0.237	0.296
Trigonia sp.	1	0.054	0.098	0.006		0.158
VIOLACEAE	10	0.539		0.112	0.474	1.124
Leonia cymosa Mart.	1	0.054	0.098	0.004		0.156
Rinorea racemosa (Mart.) Kuntze	9	0.485	0.589	0.108		1.182
VOCHYSIACEAE	45	2.423		5.226	1.896	9.545
Erisma bicolor Ducke	13	0.700	0.884	0.024		1.608
Erisma japura Spruce ex Warm.	3	0.162	0.295	1.301		1.758
Erisma splendens Stafleu	5	0.269	0.295	0.831		1.395
Erisma NCA867	2	0.108	0.196	0.001		0.305
Qualea paraensis Ducke	1	0.054	0.098	0.021		0.173
* *Vochysia guianensis* Aubl.	1	0.054	0.098	0.001		0.153
Vochysia venulosa Warm.	18	0.969	0.884	3.043		4.895
Vochysia NCA1146	2	0.108	0.098	0.004		0.209

Appendix 2. Summary diagnostics of the residuals of the time series regression analysis for estimating missing data on fruiting phenology between June and September 2001. Analyses were made through the program TRAMO (Gómez and Maravall 1997). This program handles missing observations through assigning a tentative value and specifying an additive outlier to each missing observation. The interpolation is the difference between the tentative value and the estimated regression, and it is accepted if residuals of the model are zero-mean, uncorrelated, normally distributed, with zero skewness and kurtosis, they do not contain non-linearity, and their signs are randomly distributed. The 95% critical value for each test is given in the last row.

	Mean $t(\mu_a)$	Autocorrelation Q_a	Bowman-Shenton test for normality N_a	Skewness (t)	Kurtosis (t)	McLeod & Li test on linearity Q_2	Random signs (t)
Total							
No. individuals	0.32	3.75	0.72	0.44	-0.72	12.77	-1.14
No. species	0.28	1.66	1.38	0.65	-0.98	11.40	0.38
No fruits	0.48	6.49	1.03	1.02	-0.03	7.59	1.14
Fruit mass	0.75	3.50	1.07	-0.20	-1.01	6.42	-0.38
Ripe							
No. individuals	4.99	6.88	1.12	0.22	-1.03	8.65	0.38
No. species	3.91	4.33	0.89	0.88	-0.34	5.33	-0.38
No fruits	1.12	3.26	0.91	0.51	-0.81	10.22	-
Fruit mass	1.81	4.50	0.68	-0.75	-0.35	14.33	-0.38
Climbers and epiphytes							
No. individuals	0.41	5.12	2.40	-1.48	0.47	2.14	1.14
No. species	2.79	8.15	0.96	0.21	-0.96	2.48	-0.38
No fruits	0.95	5.44	0.36	0.60	-0.03	2.75	-0.38
Fruit mass	0.80	9.14	0.12	0.31	-0.14	4.90	-0.39
Trees and palms							
No. individuals	5.70	6.27	1.65	1.26	-0.24	11.82	-2.31
No. species	0.41	6.87	0.36	-0.16	-0.57	2.45	-
No fruits	1.11	3.45	0.64	-0.44	-0.67	5.13	-0.38
Fruit mass	0.95	2.71	0.69	-0.71	-0.43	4.37	-0.39
Critical Value (95 %)	$\lvert t \rvert < 2$	< 34	< 6	$\lvert t \rvert < 2$	$\lvert t \rvert < 2$	< 34	$\lvert t \rvert < 2$

Appendix 3. Plant species bearing fruits at the canopy level recorded from December 1999 to September 2002 in a terra firme rain forest in Colombian Amazonia. N: number of fruiting individuals. T: tree, P: palm, L: liana, Ep: epiphyte, He: hemi-epiphyte, V: vine, Pa: parasite. ND = undetermined fruit mass.

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month											
							J	F	M	A	M	J	J	A	S	O	N	D
ANNONACEAE																		
Guatteria APR294		Familia de cargueros suaves	1	T	228	0.2								●	●			
Guatteria NCA1372		Familia de cargueros suaves	1	T	2100	< 0.1											●	
APOCYNACEAE																		
Couma macrocarpa Barb. Rodr.	Miya m++s+ho	Juansoco como amarillo	2	T	823	4.3				●	●			●	●			
Lacmellea arborescens (Hüll. Arg.) Markgr.	Kuuryho	Palo carcomido	4	T	6465	0.2					●	●	●	●	●			
Lacmellea foxii (Stapf) Markgraf	Taanikamoho	mi "enjebador" (chicle)	1	T	770	0.3				●	●	●						
Macoubea guianensis Aubl.	Miya n+cujee	Propio cucuy cultivado	2	T	23	103.2			●						●		●	●
Rhigospira quadrangularis (Müll. Arg.) Miers	Júvehu-m+s+o	Juansoco de alacrán	1	T	3	35.9							●					
ARACEAE																		
Heteropsis oblongifolia Kunth	Jinollu+	Bejuco yaré	1	He	1	0.2				●								
Heteropsis spruceana Schott	Jaolu	Bejuco yaré	2	He	18	0.1										●		
Philodendron megalophyllum Schott			1	He	3	17.0					●							
ARECACEAE																		
Oenocarpus bacaba Mart.	Tagaio	Milpesillo	2	P	2480	8.2					●					●		●
Socratea exorrhiza (Mart.) H. Wendl.	Igaiku	Zancona	1	P	1558	1.3	●				●					●		●
BOMBACACEAE																		
Scleronema micranthum (Ducke) Ducke	Juubuho	Acá sano (Yolombo)	6	T	2594	83.6		●	●	●	●	●	●					
BROMELIACEAE																		
Achmea tillandsioides (Mart. ex Schult. & Schult.f.) Baker		Piña de monte (Maceta)	3	Ep	93	< 0.1							●				●	●
BURSERACEAE																		
Dacryodes chimantensis Steyerm. & Maguire	Daagi-namejenehe	Laurel de mierda de perico	5	T	7326	0.6	●	●	●	●	●	●	●	●	●	●	●	●
Protium altsonii Sandwith	Maaniho	Palo de breo	7	T	22445	3.5	●	●	●	●	●	●						●
Protium apiculatum Swart	J+r+m+-meejegiho	Laurel de los pajaritos	1	T	15696	0.4			●	●	●							
Protium hebetatum Daly	Aimoo	Clase de incienso	4	T	2102	2.9	●	●	●	●	●	●			●			
Protium pilosum (Cuatrec.) Daly		Clase de incienso	2	T	2150	1.2			●	●	●	●						
Protium polybotryum (Turcz.) Engl.	Aaryubiñaho		2	T	23298	2.2	●	●	●	●	●	●						

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month											
							J	F	M	A	M	J	J	A	S	O	N	D
CAESALPINIACEAE																		
Hymenaea TPL061	Karapaho	Algarrobo	1	T	58	2.4	●	●	●	●	●	●						
CECROPIACEAE																		
Cecropia distachya Huber	Uuda-goomoho	Yarumo	1	T	107	5.2	●										●	●
Coussapoa viridifolia Cuatrec.	Gáacheu		2	T	3263	0.1	●	●										●
CLUSIACEAE																		
Calophyllum brasiliense Cambess.	Quiquícugao		1	T	101	2.4	●											●
Clusia amazonica Planch. & Triana	Jubaga-bacoco	Matapalo	6	L	665	0.7		●	●		●							
Clusia gaudichaudii Choisy ex Pl. & Tr.		Matapalo	5	L	875	1.0	●	●		●	●		●			●	●	●
Clusia grammadenioides Pipoly		Matapalo	6	L	960	0.2	●	●	●	●						●		●
Clusia hammeliana Pipoly		Matapalo	4	L	477	0.1					●	●	●					●
Clusia cf. *microstemon* Planch. & Triana		Matapalo	2	L	277	0.2	●	●										●
Clusia palmicida Rich. ex Planch. & Triana		Matapalo	1	L	120	1.0					●	●	●	●	●			
Clusia cf. *pana-panari* (Aubl.) Choisy		Matapalo	3	L	3569	0.3	●	●			●	●	●					
Clusia penduliflora Engl.		Matapalo	2	L	1888	0.1	●			●	●				●	●		●
Clusia schomburgkiana (Pl. & Tr.) Benth. ex Engl.		Matapalo	2	L	2560	0.7	●	●	●	●		●	●	●	●	●	●	●
Clusia spathulifolia Engl.		Matapalo	5	L	19415	0.1	●	●		●	●	●	●	●	●	●	●	●
Clusia viscida Engl.		Matapalo	2	L	867	4.8			●		●		●					
Clusia APR119		Matapalo	4	L	4522	0.5	●	●	●	●	●	●	●		●	●		
Clusiella cf. *pendula* Cuatrec.		Matapalo	1	L	70	0.3							●					
Moronobea coccinea Aubl.			2	T	660	ND					●	●						
Platonia insignis Mart.			1	T	39	16.6		●	●									
Tovomita cf. *brevistaminea* Engl.	Ifayinoh+-maaniho	Breo de tierra firme	1	T	900	0.6					●	●						
COMBRETACEAE																		
Buchenavia tetraphylla (Aubl.) R.A. Howard	Aamehe	Palo de hoja	5	T	32935	0.9	●	●	●	●	●	●	●			●	●	●
CONNARACEAE																		
Pseudoconnarus macrophyllus (Poepp.) Radlk.		Bejuco de venado	1	L	270	0.6						●	●					
Pseudoconnarus rhynchosioides (Standl.) Prance			1	L	140	0.1					●	●						
CONVOLVULACEAE																		
Dicranostyles cf. *altissima* (P.& E.) Bennett			2	L	1056	< 0.1					●	●	●	●	●			
Dicranostyles cf. *ampla* Ducke			1	L	686	1.6						●	●	●	●	●		

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	J	F	M	A	M	J	J	A	S	O	N	D
Dicranostyles integra Ducke			4	L	1660	1.1				●	●	●	●					
Dicranostyles cf. *scandens* Benth.			1	L	270	1.8						●	●	●				
Dicranostyles sericea Gleason			6	L	12105	1.6		●		●	●	●	●	●	●	●		
Dicranostyles APR250			3	L	3303	0.4				●	●	●	●	●	●			
Dicranostyles APR175			4	L	6461	0.9				●	●	●	●	●	●			
Maripa cf. *reticulata* Ducke		Bejuco de conga	5	L	6287	0.7		●	●	●		●	●	●	●			
CUCURBITACEAE																		
Cayaponia cf. *oppositifolia* Harms			1	V	125	2.0					●	●						
Cayaponia TPL057			1	V	53	1.3	●	●	●		●							
CHRYSOBALANACEAE																		
Licania apetala (E. Mey.) Fritsch	Jiiovo-kagiijaho	Palo de cemento ordinario	8	T	5131	2.5	●	●	●	●	●	●				●	●	●
Licania granvillei Prance		Familia de palo de cemento	1	T	228	4.4											●	
Licania cf. *heteromorpha* Benth.	Jusenee	Familia de palo de cemento	1	T	800	9.7					●	●	●	●				
Licania cf. *reticulata* Prance		Familia de palo de cemento	2	T	1398	5.0	●	●	●	●	●							
Licania cf. *subarachnophylla* Cuatrec.		Familia de palo de cemento	1	T	69	2.9			●	●								
Licania TPL072		Familia de palo de cemento	2	T	1550	2.1				●	●	●	●					
Licania APR161	Taaka-kagiijaho	Palo de cemento de sardina	1	T	429	76.3	●	●	●	●	●	●	●					●
Licania TPL068		Familia de palo de cemento	1	T	1015	0.9	●	●	●	●							●	●
DICHAPETALACEAE																		
Dichapetalum rugosum (Vahl) Prance			1	L	5	0.6					●							
DILLENIACEAE																		
Doliocarpus novogranatensis Kubitzki	Ij+m+ico		1	L	192	< 0.1					●	●						
Doliocarpus NCA268			1	L	30	3.6					●	●						
ELAEOCARPACEAE																		
Sloanea cf. *robusta* Uittien	Noobas+je	Palo bambudo de achiote silvestre	1	T	385	6.6			●	●			●	●				
ERICACEAE																		
Satyria panurensis (Benth. ex. Meisn.) Benth. & Hook.f. ex Nied.	Jubaga-bacoco	Matapalo	18	L	22524	0.1		●	●	●	●	●	●	●	●	●		●
EUPHORBIACEAE																		
Alchornea triplinervia (Spreng.) Müll. Arg	Jagijebanoho	Palo balsudo de rastrojo	1	T	1400	< 0.1									●			
Conceveiba tristigmata J.Murillo			1	T	174	0.8	●			●	●	●						●
Hevea guianenesis Aubl.	Miya-maakiniku	Siringa propia	3	T	533	12.6	●	●	●	●	●	●	●					●

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month											
							J	F	M	A	M	J	J	A	S	O	N	D
Hevea NCA1290		Clase de siringa	4	T	222	5.6	●	●		●						●	●	●
Mabea TPL118		Clase de siringa	1	T	3618	0.8			●	●	●	●	●					
Micrandra elata (Didr.) Müll. Arg.		Clase de siringa	4	T	164	7.4	●	●		●	●							
Micrandra spruceana (Baill.) R.E. Schult.		Siringa blanca	4	T	692	5.9	●	●	●	●	●	●	●	●		●	●	●
Senefeldera aff. *verticillata* (Vell.) Croizat			1	T	2467	0.3												●
Senefeldera TPL091			1	T	1126	0.8				●	●	●						
FABACEAE																		
Clathrotropis macrocarpa Ducke	Buurerehe	Palo que también babea, guama fariñero	3	T	572	66.4	●	●	●	●	●	●		●	●			
Swartzia cf. *lamellata* Ducke	Juuveuba	Costillo	1	T	80	1.0					●							
Swartzia racemosa Benth.	Daagi-gooj+	Nalga de perico	1	T	16	0.3										●		
Swartzia schomburgkii Benth.	Usuno-juuveuba	Costillo de mal olor (guama)	4	T	1279	0.3	●				●	●	●			●	●	●
GESNERIACEAE																		
Codonanthe crassifolia (H.Focke) C.V. Morton			8	Ep	155	0.1			●	●	●							
GNETACEAE																		
Gnetum cf. *leyboldii* Tul.			1	L	750	1.0					●							
Gnetum nodiflorum Brongn.			2	L	18	1.0					●							
HUGONIACEAE																		
Roucheria columbiana Hallier f.	Yaagaiho	Palo baboso y liso que se pela fácil	2	T	6278	1.1		●	●									
HUMIRIACEAE																		
Vantanea peruviana J.F. Macbr.	Juusenehe	Acá está viche	2	T	570	67.8	●		●	●		●	●	●	●	●		●
Vantanea spichigeri A.H.Gentry	Garyaryaho	Palo de pepa con ventanitas	8	T	477	23.3	●			●	●	●	●			●	●	●
Vantanea APR124	Garyaryaho	Palo de pepa con ventanitas	2	T	554	0.7	●	●		●	●			●	●	●	●	●
LAURACEAE																		
Aniba cf. *puchury-minor* (Mart.) Mez			1	T	276	0.3										●		●
Endlicheria cf. *dysodantha* (Ruiz & Pav.) Mez		Familia de ajey+	5	T	12593	0.1	●	●	●	●				●	●	●	●	●
Endlicheria cf. *sericea* Nees	Gino-aamee-+t+faño-ajey+	Palo de pepa rasquiñosa de hoja colorada	1	T	1300	0.3									●			
Licaria cf. *guianensis* Aubl.	+j+m+ho	Palo de espanto	2	T	32696	1.2				●	●	●	●	●				
Mezilaurus itauba (Meisn.) Taub. ex Mez	Meemerijeebuho	Palo para cama de ratón	3	T	494	1.1				●	●						●	●
Ocotea argyrophylla Ducke		Aguacatillo	4	T	1949	0.1	●		●	●	●					●		●
Ocotea cf. *cernua* (Nees) Mez		Familia de ajey+	1	T	102	0.2	●											●

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month											
							J	F	M	A	M	J	J	A	S	O	N	D
Ocotea NCA1256			1	T	1086	1.2				●						●		
LECYTHIDACEAE																		
Eschweilera cf. *albiflora* (DC.) Miers	Dujenee	Palo de gavilán	1	T	30	12.2								●			●	
Eschweilera coriacea (DC.) S.A. Mori		Carguero	8	T	2818	13.1	●	●	●	●	●	●	●	●	●	●	●	●
Eschweilera ovalifolia (DC.) Nied.		Carguero	2	T	118	37.2				●	●							
Eschweilera parviflora (Aubl.) Miers	Mogaje	Carguero de gavilán	2	T	123	9.5		●	●	●	●		●					
Eschweilera punctata S.A. Mori	Asehe	Palo viche	7	T	35702	4.1	●	●	●	●	●	●	●	●	●	●	●	●
Eschweilera cf. *rufifolia* S.A. Mori	Faibem+o	Carguero	1	T	95	ND				●	●							
Eschweilera tessmannii R. Knuth	Jec+m+-cugao	Popay de mochilero	2	T	267	14.7				●	●	●	●					
Eschweilera TPL119		Carguero	2	T	2416	13.0		●	●	●	●	●						
Eschweilera APR160		Carguero	1	T	398	25.8	●	●	●	●	●	●						
Eschweilera APR215		Carguero	2	T	1664	8.4	●	●	●	●	●	●	●	●				
LOGANIACEAE																		
Strychnos cf. *amazonica* Krukoff	Namitaco	Bejuco de veneno	1	L	230	5.0					●	●	●	●	●			
LORANTHACEAE																		
Oryctanthus cf. *alveolatus* (Kunth) Kuijt		Pajarito	1	Pa	13	< 0.1					●							
Phthirusa pyrifolia (Kunth) Eichler		Pajarito	2	Pa	1197	< 0.1	●	●									●	●
Phthirusa APR143		Pajarito	2	Pa	9050	1.3		●			●	●	●	●	●			
Phthirusa APR115		Pajarito	3	Pa	2718	0.1		●	●			●	●	●	●			
Psittacanthus cf. *corynocephalus* Eichler		Matapalo	1	Pa	320	0.3							●	●				
MALPIGHIACEAE																		
Brysonima APR170	T+k+m+ho	Palo de almizcle de chucha	1	T	10780	0.1					●	●						
MARCGRAVIACEAE																		
Marcgravia coriacea Vahl			2	L	4332	0.6			●	●	●	●	●	●	●	●		
Marcgravia cf. *parvifolia* Richard ex Wittm.			4	L	1062	0.4	●								●	●		●
Marcgravia punctifolia S. Dressler			2	L	444	0.9									●			
Marcgraviastrum mixtum (Triana & Planch.) Bedell			1	L	1218	0.4				●	●	●	●					
Sarcopera NCA1504			2	L	3790	< 0.1												●
Souroubea guianensis Aubl.	Tyuimiyi	Bejuco de loro	14	L	75793	0.3	●	●	●	●	●	●	●	●	●	●	●	●
MELASTOMATACEAE																		
Miconia cf. *lepidota* Schrank & Mart. ex DC.			3	T	1877	< 0.1				●						●	●	

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month											
							J	F	M	A	M	J	J	A	S	O	N	D
Miconia cf. *multispicata* Naudin			1	T	90	< 0.1										●		
Mouriri myrtifolia Spruce ex. Triana	G+s+re	Palo tieso y duro	1	T	350	0.2					●			●	●			
MELIACEAE																		
Guarea silvatica C. DC.	Jiiovo-daaginamogañoho	Palo ordinario de mierda de perico	1	T	112	1.2			●						●			
MENISPERMACEAE																		
Abuta grandifolia (Mart.) Sandwith	Namitako	Bejuco de veneno	1	L	75	1.1				●	●							
Abuta imene (Mart.) Eichler	Jeek+noogaiko	Bejuco de polvo amarillo	1	L	1550	0.2				●	●	●						
Abuta rufescens Aubl.			1	L	2581	0.5				●	●	●						
Curarea cf. *tecunarum* Barneby & Krukoff			1	L	265	1.4					●				●	●		
Curarea NCA262			2	L	23494	1.3					●			●	●			
Telitoxicum cf.*minutiflorum* (Diels) Moldenke	Jeeb+tabutako	Bejuco de veneno	1	L	1430	1.8							●	●	●			
Telitoxicum APR246			2	L	130	1.0							●	●				
MIMOSACEAE																		
Abarema leucophylla (Spruce ex Benth.) Barneby & J.W. Grimes	Jekiim+ho	Palo de mochilero	1	T	15	2.3				●								
Inga cf. *brachyrhachis* Harms (M.)	Jaakukuga-t++siho	Guamo de sapo venenoso	1	T	1010	4.7						●	●					
Inga cf. *pezizifera* Benth.	Mady+hi-t++siho	Guamo de gente antigua	2	T	553	10.6				●	●	●	●					
Inga cf. *ruiziana* G. Don	Jacucuga-t+s+o	Guama de sapo venenoso	1	T	261	1.1		●	●	●								
Inga APR182		Guama	1	T	725	4.7				●	●	●	●					
Parkia panurensis Benth. ex Hopkins	Fat+gao	Guama	2	T	3490	19.2				●	●	●	●	●				
MORACEAE																		
Brosimum guianense (Aubl.) Huber	Fecaje-guree	Palo de pepas de pava	1	T	362	0.9				●	●							
Brosimum rubescens Taub.	Faibe-k++d+h+	Granadillo	2	T	1454	0.7		●	●	●						●		●
Brosimum utile (Kunth) Pittier	M+n+ba	Vaco hoja pequeña	1	T	1020	2.5					●							
Ficus guianensis Desv. s.l.		Higuerón	1	He	1234	< 0.1										●		
Helicostylis scabra (J.F. Macbr.) C.C. Berg	Jiigaiku-ady+h+	Ojo de culebra	1	T	320	0.4					●	●						
Helicostylis tomentosa (Poepp. & Endl.) Rusby	Jigaiucu-all+noo	Ojo de culebra	1	T	1709	0.3	●	●	●	●	●							●
Pseudolmedia laevigata Trécul	Guree	Palo de pepa blandita	2	T	5089	0.3		●	●	●					●			
MYRISTICACEAE																		
Compsoneura capitellata (A. DC.) Warb.	Jiiovo-j+fahiho	Palo de sangre roja - Sangretoro	2	T	280	2.7					●						●	
Iryanthera coriacea Ducke		Mamita	1	T	710	0.3	●	●										●

Plant species	Muinane name	Spanish common name	N	Growth form	No. fruits	One fruit dry mass (g)	Fruiting month J	F	M	A	M	J	J	A	S	O	N	D
Iryanthera elliptica Ducke	N++ba-ju+m+ho	Mamita fruto grande	1	T	53	13.4				●	●	●						
Iryanthera laevis Markgr.		Mamita	1	T	280	0.6										●		
Iryanthera paraensis Huber		Mamita	3	T	9	0.6				●						●	●	
Iryanthera polyneura Ducke	N++ba jej+m+o	Mamita de sol	3	T	148	1.0	●	●								●	●	●
Osteophloeum platyspermum (Spruce ex A. DC.) Warb.	Miya-j+faiho	Propio palo de sangre roja - Sangretoro	1	T	20	8.1								●				
Virola carinata (Benth.) Warb.			1	T	22	1.5	●											●
Virola elongata (Benth.) Warb.	Juufaifim+ho-k++r+ku	Mamita de ambil de monte	1	T	1287	0.4				●		●	●	●	●			
MYRTACEAE																		
Myrcia cf. *splendens* (Sw.) DC.			2	T	8039	0.2					●	●	●		●	●		●
OLACACEAE																		
Heisteria barbata Cuatrec.	Naamom+o		1	T	50	0.2								●	●			
POLYGONACEAE																		
Coccoloba excelsa Benth.			1	L	700	0.2							●	●				
Coccoloba marginata Benth.			1	L	1081	0.7			●		●							
SAPINDACEAE																		
Matayba purgans (Poepp.) Radlk.	Gosico		1	T	200	0.9				●	●							
Talisia cf. *micrantha* Radlk.			1	T	9960	ND					●	●						
SAPOTACEAE																		
Chrysophyllum sanguinolentum (Pierre) Baehni	N+baje-bam+ho	Palo de cangrejo	9	T	1352	34.9				●	●	●	●			●	●	
Micropholis maguirei Aubrév.	Tumohom+-cajao	Yugo de paloma	1	T	903	1.0	●	●				●						
Micropholis melinoniana Pierre	Jiiovo-juriisuho	Palo hinchador ordinario	1	T	326	0.1											●	
Micropholis venulosa (Mart. & Eichler) Pierre	Juurisuho	Palo de inflamación (caimito)	1	T	750	1.9					●	●						
Pouteria guianensis Aublet.	Miya-baj+ho-m+seesehe	Propio caimo de monte	6	T	908	5.1				●	●	●	●	●				
Pouteria cf. *trilocularis* Cronquist	Fon+m+-kajaho	Yugo de dormilón	1	T	44	41.6				●	●							
Pouteria torta (Mart.) Radlk.	Jeeba-m+seesehe	Caimo de guacamaya	1	T	12	1.1										●		
Pouteria TPL089		Familia de caimo	1	T	30	9.8			●	●								
Pradosia schomburgkiana (A.DC.) Cronquist	Maragaanoho	Palo con hoja como de casabe	1	T	47	1.4											●	
VERBENACEAE																		
Aegiphila glandulifera Moldenke			1	L	32	0.1										●		

Appendix 4. Cultivated and wild fruiting trees most widely used by the indigenous community Nonuya of Peña Roja in Colombian Amazonia. Name in Muinane according to the local/traditional classification system, local name in Spanish, name according to western scientific taxonomy and fruiting month.

Plant species						Fruiting month											
			Scientific Name														
Muinane name	Group	Spanish local name	Family	Species	Cultivated or Wild	J	F	M	A	M	J	J	A	S	O	N	D
Igom+ cuj+	Aguacates	Aguacate de cusumbe	Lauraceae	*Persea americana*	Cultivated					●	●	●	●	●	●	●	
Miya cuj+	Aguacates	Propio aguacate	Lauraceae	*Persea americana*	Cultivated					●	●	●	●	●	●	●	
Baj+ho juuyaba	Anones	Anón amazónico	Annonaceae	*Rollinia* sp.	Cultivated		●										
Fik+ba	Anones	Untranslatable	Annonaceae	*Oxandra* sp.	Cultivated		●										
Kajaho visiva	Anones	Pepa de morrocoy de rebalse	Annonaceae	*Oxandra* sp.	Wild		●										
Visiva	Anones	Pepa de piedra (especie de anón pero que no se come)	Annonaceae	*Duguetia* sp.	Wild			●									
Tugu+y+	Asaí	Asaí común	Arecaceae	*Euterpe precatoria*	Cultivated			●			●	●	●		●		
Yarriga tugu+y+	Asaí	Asaí de tablón	Arecaceae	*Euterpe* sp.	Wild			●			●	●	●		●		
Faibe-k++d+h+	Bacos	Corazón de chupaflor - Granadillo	Moraceae	*Brosimum rubescens*	Wild				●								
K+b+ba	Bacos	Baco de hoja grande y ancha	Moraceae	*Brosimum longifolium*	Wild										●	●	
M+niba	Bacos	Baco hoja pequeña.	Moraceae	*Brosimum utile*	Wild	●	●		●	●					●	●	●
Ahibejetao	Barbascos	Untranslatable	Fabaceae	*Lonchocarpus* sp.	Cultivated	●	●	●	●								
Gaifirriho	Barbascos	Untranslatable	Fabaceae	*Lonchocarpus* sp.	Cultivated	●	●	●	●								
Miya tuumoho	Barbascos	Palo de paloma de centro	Caryocaraceae	*Caryocar* sp.	Wild	●	●	●	●								
Numio	Barbascos	Untranslatable	Fabaceae	*Lonchocarpus* sp.	Cultivated	●	●	●	●								
Namitaco	Bejuco	Bejuco de veneno	Loganiaceae	*Strychnos* cf. *amazonica*	Wild	●				●	●			●			●
Macam+o	Caimos	Caimo pepa grande	Sapotaceae	*Pouteria* sp.	Cultivated						●	●	●	●		●	●
Miya m+sesehe	Caimos	Propio caimo cultivado	Sapotaceae	*Pouteria caimito*	Cultivated						●	●	●	●		●	●
N+ba m+sesehe	Caimos	Caimo de cangrejo - Palo de balata	Sapotaceae	*Manilkara* sp.	Wild					●							
Tuuj+ m+sesehe	Caimos	Caimo de lombriz	Sapotaceae	*Chrysophyllum prierurii*	Wild								●	●			
Curruba inoo	Cananguchos	Canangucho de azafrán	Arecaceae	*Mauritia* sp.	Wild				●	●	●	●	●				
Tuje inoo	Cananguchos	Canangucho baboso de oso hormiguero	Arecaceae	*Mauritia* sp.	Wild				●	●	●	●	●				
Uyuta inoo	Cananguchos	Canangucho de gusano lanudo y rojo	Arecaceae	*Mauritia flexuosa*	Wild				●	●	●	●	●				
Viyduo inoo	Cananguchos	Canangucho largo de hacer trompo	Arecaceae	*Mauritia* sp.	Wild				●	●	●	●	●				
Cajaho k+boj+hucu	Cargueros	Carguero de rebalse	Annonaceae	*Guatteria* sp.	Wild			●									

Plant species						Fruiting month											
		Scientific Name															
Muinane name	Group	Spanish common name	Family	Species	Cultivated or Wild	J	F	M	A	M	J	J	A	S	O	N	D
Cajao Mogaje	Cargueros	Palo de gavilán de rebalse	Lecythidaceae	*Eschweilera* sp.	Wild	●	●	●									
Dujenehe	Cargueros	Palo de amarrar	Lecythidaceae	*Eschweilera* cf. *albiflora*	Wild	●	●	●									
Faibem+ho dugenehe	Cargueros	Hoja finita y larga, resistente y suave	Lecythidaceae	*Eschweilera* cf. *rufifolia*	Wild	●	●	●									
Firraje dugenehe	Cargueros	Palo de mojarrilla pequeña amarillenta	Lecythidaceae	*Eschweilera* sp.	Wild	●	●	●									
Gadamehu dugecu	Cargueros	Palo de matafrío	Lecythidaceae	*Eschweilera* sp.	Wild	●	●	●									
K+boj+ucu dugenehe	Cargueros	Carguero negro de rastrojo	Annonaceae	*Guatteria* sp.	Wild										●	●	
Matam+ho	Cargueros	Palo de chilaco de centro	Lecythidaceae	*Eschweilera* sp.	Wild	●	●	●									
Mogaje	Cargueros	Carguero de gavilán	Lecythidaceae	*Eschweilera parviflora*	Wild	●	●										
Nivigai dujecu	Cargueros	Carguero de venado	Annonaceae	*Xylopia excellens*	Wild										●		●
Saarrim+ho dugecu	Cargueros	Sirve para matafrío	Lecythidaceae	*Eschweilera* sp.	Wild	●	●	●									
J+cunigai geryehe	Castaño	Castaño cabeza de tigre	Lecythidaceae	*Cariniana decandra*	Wild										●		
Jimuai nigai jeryehe	Castaño	Cabeza de mico tanque	Lecythidaceae	*Cariniana* sp.	Wild										●		
Gaño nicuje	Cucuy	Cucuy de monte	Apocynaceae	*Macoubea guianensis*	Wild	●	●	●									
Miya n+cujee	Cucuy	Propio cucuy cultivado	Apocynaceae	*Macoubea guianensis*	Cultivated	●	●	●									
Paatd+ba momoho	Chontaduro	Chontaduro de pepa amarilla	Arecaceae	*Bactris* sp.	Cultivated	●	●	●									●
Taava momoho	Chontaduro	Chontaduro rojo	Arecaceae	*Bactris gasipaes*	Cultivated	●	●	●									●
Tuguiy+ momoho	Chontaduro	Chontaduro que no tiene espina	Arecaceae	*Bactris* sp.	Cultivated	●	●	●									●
Ajey+	Familia de palo de guara	Palo rasquiñoso	Lauraceae	*Endlicheria* sp.	Wild										●	●	
Fat+ba	Familia de palo de guara	Palo de guara	Lauraceae	*Licaria* cf. *guianensis*.	Wild	●	●										●
Taava mejeguiho	Familia de palo de guara	Laurel de pescado (familia de ajey+)	Lauraceae	*Nectandra* cf. *egensis*	Wild				●	●							
Gu+s+rr++	Gu+s+rr++	Untranslatable	Myrtaceae	*Eugenia* sp.	Wild							●					
Gu+s+rr+t+rr+y+	Gu+s+rr++	Untranslatable	Melastomataceae	*Mouriri myrtifolia*	Wild				●	●							
Fa-cum+ho	Guacury	Guacury rojo.	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
Kik+ juvehe	Guacury	Cabeza de murciélago	Icacinaceae	*Poraqueiba* sp.	Cultivated		●	●									
Miya juvehe	Guacury	Especie de guacury sembrado	Icacinaceae	Icacinaceae sp.	Cultivated		●	●									
N+facaho	Guacury	Propio guacury de pepa verde	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
N+facaho Niveet+ho	Guacury	Guacury entre amarillo y verde	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									

Plant species						Fruiting month											
			Scientific Name														
Muinane name	Group	Spanish common name	Family	Species	Cultivated or Wild	J	F	M	A	M	J	J	A	S	O	N	D
N+facaho Tu-rruga	Guacury	Guacury morado o negro	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
T++faño niim+	Guacury	Guacury anaranjado (cultivado)	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
T++faño niveet+ho	Guacury	Guacury entre amarillo y verde	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
T++faño turruga	Guacury	Guacury morado o negro	Icacinaceae	*Poraqueiba sericea*	Cultivated		●	●									
Taava niim+ho	Guacury	Guacury de pescado	Icacinaceae	*Poraqueiba* sp.	Cultivated		●	●	●								
Y+-j+ho	Guacury	Guacury de pepa pequeña, silvestre	Icacinaceae	*Poraqueiba* sp.	Cultivated		●	●									
Bua t+si	Guamas pequeñas y silvestres	Guama de boa - guama pequeña de orilla de río	Mimosaceae	*Inga longifoliola*	Wild				●								
C+m+ ibugano	Guamas pequeñas y silvestres	Guamo de cola de churuco	Mimosaceae	*Inga* sp.	Wild				●								
Gacham+ ibugano	Guamas pequeñas y silvestres	Guamo de cola de mico nocturno	Mimosaceae	*Inga* sp.	Wild				●								
Iyu ibugano	Guamas pequeñas y silvestres	Guamo de cola de cotudo	Mimosaceae	*Inga* sp.	Wild				●								
Jacucuga t+si	Guamas pequeñas y silvestres	Guamo de sapo	Mimosaceae	*Inga* cf. *ruiziana*	Wild				●								
Buam+ho	Guamos cultivados	Guamo grueso y corto	Mimosaceae	*Inga* sp.	Cultivated	●			●	●			●		●		
Ja-jebaho	Guamos cultivados	Guamo plancheto y un poco peludo	Mimosaceae	*Inga* sp.	Cultivated	●			●	●			●		●		
T+s+o j+gom+ho	Guamos cultivados	Guamo largo cultivado	Mimosaceae	*Inga edulis*	Cultivated	●			●	●			●		●		
Fat+gaho	Guamos silvestres	Palo de guara (guamo)	Mimosaceae	*Parkia panurensis*	Wild	●	●	●									
T+burruo	Guamos silvestres	Guamo en racimos	Mimosaceae	*Parkia* sp.	Wild	●	●	●									
Bumomom+	Higuerones	Palo rojizo sólo en canaguchales	Moraceae	*Ficus* sp.	Wild	●	●	●						●			●
Jigayuje gachehu	Higuerones	Hoja rojiza	Moraceae	*Ficus* sp.	Wild	●	●	●									●
Muuaio gachehu	Higuerones	Higuerón ordinario	Moraceae	*Ficus* sp.	Wild	●	●	●						●			●
N+-cuje gacheu	Higuerones	Hoja grande como de cucuy	Moraceae	*Ficus* sp.	Wild	●	●	●			●			●			●
Sese ihaño	Higuerones	Palo blanco	Moraceae	*Ficus* sp.	Wild	●	●			●	●			●			●
Curriba	Juanzoco	Juanzoco pepa grande poco rojizo	Apocynaceae	*Couma* sp.	Wild			●	●								
Jubeho curriba	Juanzoco	Juanzoquillo de alacrán	Apocynaceae	*Rhigospira quadrangularis*	Wild			●	●								

Plant species																	
			Scientific Name			Fruiting month											
Muinane name	Group	Spanish common name	Family	Species	Cultivated or Wild	J	F	M	A	M	J	J	A	S	O	N	D
Miya m++s+ho	Juanzoco	Juanzoco como amarillo	Apocynaceae	*Couma macrocarpa*	Wild	●		●									
N+ba curriba	Juanzoco	Juanzoquillo grande café	Apocynaceae	*Couma* sp.	Wild			●	●								
D+da mejegiho	Laureles	Laurel de pepa grande	Burseraceae	Dacryodes sp.	Cultivated							●					
Daagi mejegiho	Laureles	Laurel pequeño	Burseraceae	Dacryodes sp.	Cultivated							●					
Miya mejegiho	Laureles	Laurel propio	Burseraceae	*Dacryodes peruviana*	Cultivated							●					
Oco amene maniho	Madroño	Madroño grande	Clusiaceae	*Garcinia* sp.	Cultivated		●	●	●								
Unumenene maaniho	Madroño	Madroño pequeño	Clusiaceae	*Garcinia madruno*	Cultivated		●	●	●								
Caadu ju+m+ho	Mamitas	Semilla rosada	Myristicaceae	*Iryanthera* sp.	Wild	●	●	●									
Cajaho ju+m+ho	Mamitas	Mamita de rebalse	Myristicaceae	*Virola* sp.	Wild		●	●	●								
Juufaifim+ho	Mamitas	Sangre de toro	Myristicaceae	*Virola elongata*	Wild	●	●	●									
Miya ju+m+ho	Mamitas	Propio mamita	Myristicaceae	*Iryanthera laevis*	Wild	●	●	●									
N++ba jej+m+o	Mamitas	Mamita de sol	Myristicaceae	*Iryanthera polyneura*	Wild	●	●										●
N+baje ju+m+ho	Mamitas	Mamita de cangrejo	Myristicaceae	*Iryanthera polyneura*	Wild	●	●	●									
Piryijao	Mamitas	Palo de entorchar - pepa pequeña color amarillo	Myristicaceae	*Iryanthera ulei*	Wild	●	●	●	●								
Tuim+ jaho	Maraca	Maraca de lorito	Sterculiaceae	*Theobroma* sp.	Cultivated			●									
Añaaje	Marañón	Marañón grande	Anacardiaceae	*Anacardium giganteum*	Cultivated			●	●	●							
Marr+ganoho	Marr+Ganoho	Untranslatable	Rhizophoraceae	*Sterigmapetalum* sp.	Wild												●
Gaanao	Medio cominos	Medio comino de hoja corta.	Lauraceae	*Ocotea* sp.	Wild										●	●	●
K+m+o	Medio cominos	Palo de manguare	Lauraceae	*Ocotea* sp.	Wild										●	●	●
N+n+m+o	Medio cominos	Medio comino – Cachorro de quebrada	Lauraceae	*Ocotea* sp.	Wild									●	●	●	●
Noobao	Medio cominos	Palo de achote	Lauraceae	*Ocotea* sp.	Wild										●	●	●
Cuume	Milpesos	Milpeso común	Arecaceae	*Oenocarpus bataua*	Wild				●	●	●	●					
Cuume	Milpesos	Milpeso común	Arecaceae	*Oenocarpus bataua*	Wild				●	●	●	●					
Qu+rr+yaje cuume	Milpesos	Carnaza morada	Arecaceae	*Oenocarpus* sp.	Wild				●	●	●	●					
Tuuje cuume	Milpesos	Carnaza blanco	Arecaceae	*Oenocarpus* sp.	Wild				●	●	●	●					
Muaio jadio	Palo de algodón	Algodón de orilla del río	Bombacaceae	*Pseudobombax septenatum*	Wild								●	●			
Niibam+ +m+ho	Palo de babilla	Palo de babilla	Sapotaceae	Sapotaceae sp.	Wild				●	●							
Miya maanio	Palo de breo	Breo propio	Burseraceae	*Protium gallosum*	Wild											●	●
Jarracaho	Palo de cucha	Palo de cucha	Fabaceae	*Macrolobium* sp.	Wild	●	●	●									

Appendix 4. *cont.*

Plant species																	
			Scientific Name			Fruiting month											
Muinane name	Group	Spanish common name	Family	Species	Cultivated or Wild	J	F	M	A	M	J	J	A	S	O	N	D
Másacao	Palo de maní	Palo de maní	Euphorbiaceae	*Alchornea* sp.	Wild								●	●	●		
Jadijebanoho	Palo de rastrojo	Árbol de pepa negra de pescar	Anacardiaceae	*Tapirira guianensis*	Cultivated		●	●	●								
Jadijebanoho	Palo de rastrojo	Palo balsudo de rastrojo	Euphorbiaceae	*Alchornea triplinervia*	Cultivated		●	●			●			●	●		
Nib+rr+ho	Palo de rastrojo	Untranslatable	Euphorbiaceae	*Alchornea* sp.	Cultivated									●	●		
Caajano ajey+	Palo de rebalse	Baboso y rasquiñoso	Lauraceae	*Endlicheria* sp.	Wild			●	●								
Can+fio taava	Palo de rebalse	Untranslatable	Euphorbiaceae	Euphorbiaceae sp.	Wild		●	●									
J+s+cu jaho	Palo de rebalse	Maraca de caracol	Sterculiaceae	*Theobroma* sp.	Wild		●	●									
Taava j+sarracu	Palo de rebalse	Untranslatable	Chrysobalanaceae	*Licania* sp.	Wild		●										
Nicomoho	Pega-pega	Pega - pega	Apocynaceae	*Lacmellea arborescens*	Wild								●				
T+e nim+ho	Pomarosa	Guacury de danta - Pomarrosa	Melastomataceae	*Bellucia grossularioides*	Cultivated	●	●	●							●	●	●
Cugao	Popay	Propio popay	Lecythidaceae	*Eschweilera* sp.	Wild	●	●										
Jec+m+ cugao	Popay	Popay de mochilero	Lecythidaceae	*Eschweilera tessmannii*	Wild	●	●										
Quik+cugao	Popay	Popay de sapo quik+.	Sapotaceae	*Micropholis guyanensis*	Wild								●				
Taava masaca	Reventilla	Maní de pescado – Rreventilla	Euphorbiaceae	*Mabea nitida*	Wild	●	●										
M+meuje bacuho	Uvas	Uva de sapo plancheto cultivado	Cecropiaceae	*Pouroma cecropiifolia*	Cultivated	●	●			●	●	●					●
T+e ay+no baacu	Uvas	Uva de ojo de danta	Cecropiaceae	*Pouroma bicolor*	Cultivated	●	●			●	●	●					●

Appendix 5. Most common fruit eating animals studied from the local/traditional Nonuya perspective in Colombian Amazonia. The species are presented according to the local/traditional classification system. Since several animal species could not be translated or classified into the western scientific taxonomy, only for the general groups a scientific name was assigned. The local name in Spanish is also given.

Group	Muinane name	Spanish local name
Dantas (Tapiridae)		
	Cat+ t+e	Danta de pintura negra
	Gaim+je t+e	Danta de pintura morada
	Nofaij+ t+e	Danta de flor blanco
	M+sese t+e	Danta de caimo
	Gomo t+e	Danta de yarumo ordinario
Puercos (Tayassuidae)		
	C+bom+ menim+	Puerco pequeño de cachete blanco convertido de gente
	Igecu menim+	Puerco de platanillo
Cerrillos (Tayassuidae)		
	Samaiba	Cerillo que anda en par
	Obajac+maije fafaim+	Propio cerrillo pequeño que anda en manada
	Dogita	Cerrillo mediano que también anda en manada
Borugos (Agoutidae)		
	Jacu tac+	Borugo de maraca
	Nobai tac+	Borugo de pepa de achote
	Curruba tac+	Borugo de azafrán un poco amarillo y grande
	Jurruba tac+	Borugo agüeros
Guaras (Dasyproctidae)		
	Fat+gaij+ fat+	Guara del fruto de guamo negro
	M+ni fat+	Guara negra convertida de gusano m+ni
	Neje fat+	Guara de pepa de coco un poco canosa
Tintines (Dasyproctidae)		
	Gue gue j+c+mo	Tintín mediano con pecho blanco
	J+c+mo	Tintín del fruto pequeño de guamo negro
	Mei j+c+mo	Tintín convertido del hijo de diablo
Armadillos (Dasypodidae)		
	Jubo go+	Armadillo negro por encima
	Cumell+	Armadillo pequeño
	Duutu go+	Armadillo propio un poco más grande
	Gaadaba go+	Armadillo blanco de centro
	N+guiba	Armadillo trueno
Venados (Cervidae)		
	Jiibai	Venado pardo, pecho blanco
	Nibigai	Venado colorado
	Bobay+ jiibai	Venado pardo pequeño
Ratones (Muridae)		
	Miya guifo	Ratón grande pecho blanco, con cola común
	Tuco+	Ratón pequeño
	Jiburra	Ratón sin cola
	Ñarraje	Ratón con el pecho oscuro
	Uuda	Ratón lanudo grande negro
	Jacu	Ratón chuzado, cola lanuda
Ardillas (Sciuridae)		
	Chikir+	Ardilla pequeña
	Nefik+	Ardilla grande colorado
	Títiu	Ardilla pequeña familia pielroja
Micos (Cebidae, Callithrichidae)		
	Jaadio k+m+	Churuco grande un poco mono blanco
	Pecuje k+m+	Churuco pequeño negro
	Gaacheu k+m+	Churuco mediano gris
	Uyuta k+im+	Churuco grande colorado, rojizo - amarillento

Group	Muinane name	Spanish local name
	Iyu	Cotudo aullador
	Chuyiyi	Maicero color café
	J+muai	Mico tanque color amarillento
	Gacha	Mico nocturno grande que anda solo
	To’om+	Mico nocturno grande que anda solo y le gusta gritar en la noche
	Gái	Mico sogui –sogui
	Piy+m+	Mico chichico color amarillo pálido un poco blanco
	Miya jusarri	Propio bebeleche
	+g+m+ jusarri	Bebeleche grande color café
Guacamayas y Loros (Psittacidae)		
	Jeeva	Guacamaya roja
	Ino,ai	Guacamaya azul con pecho amarillo
	Ereda	Guacamaya pequeña color verde claro
	Curraba	Loro churuquero
	Curram+	Loro frente rojo
	Garru	Loro frente amarilla
	Tdui	Loro llorón con la cabeza azul
	Chr+m+	Pivicho
Pavas y Paujiles (Cracidae, Psophiidae)		
	Jaadi nim+cu	Paujil propio cola blanco
	Faicum+ nim+cu	Paujil crespo de manicuera
	Miiju	Paujil camarana
	K+j+gai nim+cu	Paujil colorado de candela
	Fecaje	Pava cabeza blanca
	K+gao	Pava colorada
	Jajeho	Pava cucunuco
	Gatarracu	Guacharaca
	Deenehe	Tente
Tucanes (Ramphastidae)		
	Miya n+go	Picón propio, pico amarillo y negro
	Jajeba n+go	Picón de puy grande
	R+hu	Picón pequeño
	Fardigai	Picón pequeño con el pecho amarillo y negro
Mochileros (Icteridae, Corvidae)		
	Cúdi jek+	Mochilero grande que anda solo
	Miya jek+m+	Mochilero propio, grande color café
	Muaio jek+m+	Mochilero pequeño, que anda en manada pico amarillo
	+g+m+ jek+m+	Mochilero pequeño negro, color rojo la parte superior de la cola
	Búa jek+	Mochilero de boa, mediano color gris
	Ñurrai	Ave color azul gris - Tía-tía
Gallinetas y Panguanas (Tinamidae)		
	K+ñu	Gallineta propia de terraza baja
	Túnu	Gallineta propia de monte firme
	Juu+	Panguana de monte firme
	Tupacu+	Panguana de terraza baja y bosque inundable
	S+rú+	Panguana pequeña de terraza baja y bosque inundable
	Y+i	Panguana pequeña de terraza baja y bosque inundable
	Fifigai	Panguana pequeña
	Firratuno	Panguana pequeña, con la carne morada

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