Fruit availability and seed dispersal in terra firme rain forests of Colombian Amazonia

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1. GENERAL INTRODUCTION

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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 Caqueta River region. Therefore, scientific research and information should be linked to the information needs of the different stakeholders (Rodriguez 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 Caqueta 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.
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, Londono-Vega and Alvarez-Davila 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, Areaceae and Dipterocarpaceae (Castaño-A. 2003, Londoño-Vega and Alvarez-Davila 1997; Appendix 1).

The forest understory is from 0 to 15 m high. Understory species include *Lepidocaryum temue* (Areaceae), *Attalea racemosa* (Areaceae) 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 Caqueta 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 Piraparana 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 monacuus 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 (Rodriguez 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.