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Introduction

Ana Catalina Londoño Vega

1.1 The importance of Amazonian forests

The Amazon Basin, which encompasses the catchments of the Amazon River and the rivers of the Guiana Shield that drain into the Atlantic Ocean, and a substantial part of the basin of Orinoco River, is covered by the largest continuous area of tropical forests in the world. Amazonian forests represent the habitat for about one-tenth of all species of the world. As such, the Amazon Basin has a fundamental role in the origin and conservation of genetic resources worldwide. However, Amazonian forests, just as most of the tropical forests in Africa and Asia, are severely threatened by mankind. Deforestation rates of humid tropical forests vary around 142,000 km² per year (FAO 2001; Achard et al. 2002; Fearnside and Laurance 2003). In the past two decades increasing attention has been paid to the important role of the Amazon Basin in Global Change, especially regarding climate change, the cycling of water and carbon, and the emission of greenhouse gasses (Junk and Furch 1985; Phillips et al. 1998; Canadell et al. 2000; Watson et al. 2000; Holmgren et al. 2001; Houghton et al. 2001; Clark et al. 2003; Malhi and Phillips 2004). Changes in atmospheric CO₂ concentrations probably influence the composition, diversity and dynamics of the forests (Clark et al. 2003; Laurance et al. 2004). It is in this context that studies about the biomass and carbon fixation of tropical forests are being intensified in recent years (Brown 1997; Silver et al. 2000; Brown 2002). Most of these studies depend on measurements of forest productivity in permanent plots, which is often estimated on the basis of yearly tree growth by diameter increments and tree mortality.

1.2 Permanent plots to study long-term forest dynamics

The adequate conservation of tropical forests and wise use of their natural resources depend to a large extent on our knowledge of the variation in these forests, both in space and in time. Long-term studies in permanent forest plots consisting of repeated surveys in well-demarcated and geo-referenced plots, allow the quantification of the temporal variation of forest resources (Campbell et al. 2002). Non-permanent plots to describe Amazonian forests along environmental gradients have been used successfully in exploratory surveys (Gentry 1988b; Duivenvoorden and

Lips 1993; ter Steege et al. 2003; Duque 2004; Benavides 2010). Yet, such plots have the disadvantage that they, similar to a photograph, only provide a limited view at a certain time. In contrast, permanent plots not only admit a detailed description of the habitat at a particular site, but also allow detecting temporal changes in the forest. Such information is indispensable to predict future changes in the diversity and distribution of species (Losos and Leigh 2004). Beyond the initial inventory of the vegetation in permanent plots it is necessary to measure forest changes in the long run, through continuous monitoring of the floristic composition, structure, growth, mortality and survival of species, preferably at more than one site (Comiskey et al. 1999).

Permanent plots have been used extensively to study long-term changes of vegetation and the natural processes that allow the coexistence of species in relation to the environment (Bakker et al. 1996; Herben 1996; Rees et al. 2001; Hubbell 2004). Early studies conducted in tropical forests primarily aimed at measuring the diameter growth for silvicultural management and timber harvesting (Bell 1971). Recent studies include other objectives such as quantifying carbon stocks and their relation to global flows (Dallmeier 1992; Phillips et al. 1998; Orrego et al. 2003). The oldest plots in tropical forests stem from the first part of the twentieth century, and were established in Philippine dipterocarp forests (Richards 1952), on the islands of Trinidad and Tobago (Bell 1971), in Peninsular Malaysia (Manokaran and Swaine 1994) and in Uganda, Africa (Sheil et al. 2000). The largest plots (25 to 50 ha) are now part of the CTF network (Center for Tropical Forest Science) of the Smithsonian Tropical Research Institute (STRI) (Losos and Leigh 2004), which manages, for example, the well-known plot on Barro Colorado Island (Panama). Another network is that by the Amazon Forest Inventory Network (RAINFOR) (Malhi et al. 2002; Malhi and Phillips 2004), which mostly supports 1-ha plots.

In Colombia, permanent forest plots were initially installed to monitor growth of timber species like *Cupressus lusitanica* (Tschinkel 1972; del Valle 1979), *Cordia alliodora*, *Tectona grandis*, *Eucalyptus saligna*, and *Cariniana pyriformis*. In the 1980's permanent forest plots were started in the Chocó region (western Colombia) (González et al. 1991; González 1995; del Valle 1996a, 1998ab, 1999) and Amazonia (Londoño 1993, this dissertation). In 2000 about 70 permanent plots were being maintained

(Vallejo et al. 2005; Álvarez et al. 2008). By mid 2006, these plots covered at least 100 ha. Overall, the two plots described in this dissertation have particular significance as they are among the oldest permanent forest plots in Colombian Amazonia, and in Colombia as a whole.

1.3 Floristic and ecological research in the permanent forest plots at Peña Roja

Between 1986 and 2000 the Tropenbos-Colombia Programme supported forest ecological research in the mid catchment of the Caquetá River, with its epicenter in Araracuara (Fig. 1-1). The programme started with a land unit survey of a large area (10,000 km²), east of Araracuara. Based on the ecological maps (Duivenvoorden and Lips 1993, 1995) in late 1988 several sites were selected as representative for the principal land units, in order to develop long-term monitoring studies of forest ecosystem functioning. The following selection criteria were applied: a) Representation: the land unit should have a wide cover in the Middle Caquetá area and in the Colombian Amazon as a whole, b) Accessibility: the site should be well accessible by river from Araracuara to allow efficient transport of personnel and equipment, c) Control, surveillance and security: sites should offer some protection for permanently installed research equipment (Duivenvoorden and Lips 1990). The sites selected were located in the area of Nonuya community of Peña Roja. One site belonged to the land unit classified as Tertiary Sedimentary Plain and the other site was located on a rarely inundated flood plain of the Caquetá River (Duivenvoorden and Lips 1990). With all parties involved it was agreed to develop a long-term research on the flora, structure and dynamics of the forest vegetation at these two monitoring sites. At each site a permanent plot of 1.8 ha was established for the long-term study of the forest. Uniform criteria were used for the establishment, i.e. the sites were chosen in such a way that very large (multiple tree gaps by wind throw) canopy gaps were avoided. Also, the physiography, forest (Duivenvoorden et al. 1988) and soils were as homogeneous as possible. From that moment on, in and outside these plots, a series of ecological studies have been successfully carried out by students from Colombia and other nationalities, for example those regarding plant-animal relationships

(van Dulmen 2001; Parrado 2005), hydrology (Téllez 2003) and nutrient cycling (Tobón 1999; Tobón et al. 2004ab).

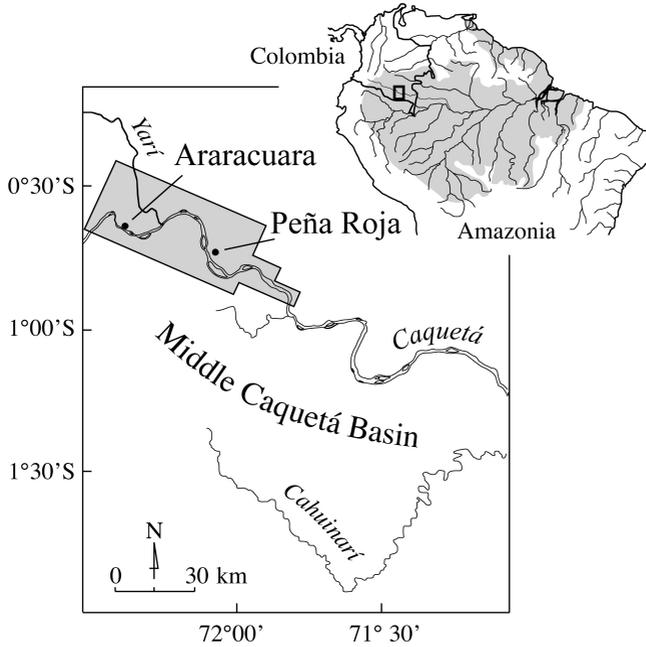


Fig. 1-1. Location of Araracuara in Colombian Amazonia. The shaded area around Araracuara and Peña Roja is given in more detail in Fig. 2-1.

There is no doubt that the activities of Tropenbos-Colombia triggered the intensification of the botanical explorations in Colombian Amazonia. In spite of considerable progress in the past years (Sánchez 1997; Rudas and Prieto 2005) it is still common that about one fifth of the species encountered in Amazonian forest surveys remains unidentified. Also, most identifications rely on sterile specimens. Therefore, the contribution of taxonomy to describe and categorize the species diversity of Amazonian forests is of utmost importance. Obtaining fertile botanical specimens of tree species is a challenge in tropical forests, because many species are sterile during a large part of the year. More importantly, many tree species are hard to encounter during botanical surveys because of their scattered occurrence in small populations. In this regard, the discovery of a new species of the family of Dipterocarpaceae, in one of the permanent plots established in the Peña Roja community was an extraordinary event. Before this discovery, the family of Dipterocarpaceae, which belongs to

one of the most dominant, species rich, and economically important tree families in tropical forests of Asia (Whitmore 1975; Ashton 1982), was only represented by one single species in the Neotropics (*Pakaraimaea dipterocarpacea* Maguire & Ashton recorded in Guyana). The record of *Pseudomonotes tropenbosii* Londoño, Álvarez and Forero in the upland plot near Peña Roja along the Caquetá river emphasizes the phytogeographical links of Colombian Amazonia with the Guiana Shield region (Duivenvoorden and Lips 1995) and even with Africa and Madagascar (via the subfamily Monotoideae; Morton 1995), and underscores the unique position and value of this permanent plot.

The architecture of a plant is the morphological expression of its genome in a given time, and a result of the balance between endogenous growth processes and exogenous constraints exerted by the environment (Barthélémy et al. 1991; Hallé 1995). The objective of architectural analysis is to identify the endogenous processes that control growth and shape of the whole plant, by means of observation. Three key concepts have been developed: the architectural model (Hallé and Oldeman 1970), the architectural unit (Édelin 1977) and the reiteration (Oldeman 1974). The concepts of model and reiteration unit have provided a valuable tool for studying the structure and form of plants. Plant architecture further determines how resources are allocated in plants, for example, regarding the capture of light, water transport, mechanical stability, and resistance to wind (Vester 1997; Poorter and Werger 1999). Vester (1997) analyzed successive architectural development of tree taxa in successional forests near Araracuara. He showed that on the basis of detailed observations, architectural analysis yields understanding of the mechanisms of succession in secondary forest or in old-growth forests. Architectural analysis thus has the potential to supply significant information regarding forest dynamics in permanent plots, to complement the demographic information of recruitment, growth and mortality.

Arguably, two principal results emerged from the ecological surveys of the Middle Caquetá area (Duivenvoorden and Lips 1993, 1995; Urrego 1997; Quiñones 2002; Duque 2004; Sánchez 2005; Benavides 2010). The first was the clear recognition of the high tree species diversity per unit of area (Valencia et al. 1994; Duivenvoorden 1996), which ranks among the highest level for tropical forests worldwide. Several explanations for the

high upper Amazonian tree species diversity have been put forward (Duivenvoorden 1995; ter Steege et al. 2006). In most of these, the unique properties of the geological setting (speciation triggered by the unique configuration and the highly dynamic environment in the Tertiary; Hoorn and Wesselingh 2010) and the climatic history of northwestern Amazonia (continuous high humidity throughout the Pleistocene favouring species survival; Lips and Duivenvoorden 1994; Mayle et al. 2004) play a key role. The second result was the evidence and documentation that forest composition and forest diversity systematically changed across land units, which differed regarding flooding, drainage and soil nutrient concentrations. High levels of forest diversity were consistently recorded in the well-drained uplands (Duivenvoorden 1996; Duivenvoorden and Duque 2010). On the other hand, poor drainage, seasonal flooding and extremely low levels of soil nutrient availability were always associated with low levels of tree species diversity (Urrego 1997; Duivenvoorden and Duque 2010). Furthermore, litterfall measurements in combination with studies of the standing stock of litter on the forest floor indicated that the aboveground decomposition of organic matter (a proxy of net primary above-ground forest productivity; Vogt et al. 1998) was substantially higher in floodplains of the Caquetá than in well-drained uplands (Lips and Duivenvoorden 1996). Summarizing, in view of the physiographic setting of the two permanent forest plots at Peña Roja, a general picture emerged from the ecological survey that soil fertility, forest disturbances, and above-ground forest productivity in floodplains of the Caquetá River were higher than in the well-drained uplands. However, because these survey results were not based on permanent plots, information about forest dynamics could not be incorporated. In more recent studies in Amazonia at continental scales, forest dynamics have been correlated with forest diversity. Wide-scale correlations between tree mortality (Phillips et al. 2004), wood specific gravity (Baker et al. 2004), above-ground biomass (Baker et al. 2004; Mahli et al. 2006), above-ground wood productivity (Mahli et al. 2006) and tree species diversity (ter Steege et al. 2006) have been reported along geological gradients from eastern Amazonia to upper Amazonian watersheds. In short, low diversity forests were associated to low levels of forest dynamics (low mortality, low productivity) and low levels of soil fertility, whereas high diversity forests showed a relatively

high mortality (and high wood productivity) and were found on relatively rich soils. Is this general scheme, obtained from Amazonia as a whole, useful to predict forest dynamics and forest diversity in a spatially more limited area like that of Colombian Amazonia?

1.4 Aims and outline of this dissertation

The principal aim of this dissertation is to provide basic knowledge about the structure, species composition, and forest dynamics of two permanent forest plots established in contrasting land units (upland and floodplain), in the central part of Colombian Amazonia. In Chapter 2 a description of the two plot sites is given, including details of the plot design and set-up. This information serves as background to the next chapters, but is also essential to warrant a sound continuation of the monitoring activities in the coming decades. Chapter 3 reports on the discovery and description of the new genus and species of the family Dipterocarpaceae that appeared as one of the more dominant species in the upland plot. Chapter 4 gives a treatment of the architecture of three subcanopy species of the nutmeg family (Myristicaceae), a pantropical family of mostly tree species. It describes the development of these species from seedlings in the undergrowth to senile trees. The main purpose of this chapter was to evaluate the extra value of architectural analysis for studies regarding forest dynamics in permanent plots. The following two chapters give accounts on the species composition (Chapter 5) and forest dynamics (Chapter 6) in the two permanent plots. Which species, genera and families characterize these plots? How is the distribution of taxa among families and genera? What is the species composition relative to the habits or growth forms? How are the modes of death? Do mortality and recruitment differ between the plots? Do the patterns in tree species composition and forest dynamics in the plots correspond to predictions based on the general model of Amazonian forest diversity as function of geology? Finally, in Chapter 7 a synthesis is given, followed by the summaries in English, Spanish and Dutch and the appendices.