Flora and dynamics of an upland and a floodplain forest in Peña Roja, Colombian Amazonia
= Flora y dinámica de bosques de tierra firme y de várzea en Peña Roja, Amazonia colombiana

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Citation for published version (APA):
Londono Vega, A. C. (2011). Flora and dynamics of an upland and a floodplain forest in Peña Roja, Colombian Amazonia = Flora y dinámica de bosques de tierra firme y de várzea en Peña Roja, Amazonia colombiana.

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Site description of the upland and floodplain plots

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2.1 Location and accessibility

The permanent plots are located about 30 km east (and 70 km downstreams) of Araracuara (Fig. 2-1), in the basin of the Caquetá River, Colombian Amazonia. This area is part of the community of Peña Roja (Nonuya ethnicity), which is under the jurisdiction of the so-called Corregimiento de Puerto Santander, Departamento del Amazonas. The access to Araracuara from Bogotá is by air. Reaching the upland plot requires about 2 km walking from the maloca in Peña Roja. The floodplain plot can be reached by river, navigating upstream along the Caquetá river from the maloca in Peña Roja for about 2.5 km and then walking ca. 0.5 km.

2.2 Climate

The information about the current climate in the study area is based on two meteorological stations: one in Araracuara and one in Peña Roja. At Araracuara daily records were available from 1979-1990 (station code 4413501 located at 160 m altitude above sea level; Duivenvoorden and Lips 1995). Climate data from Peña Roja were automatically recorded every 20 minutes between November 1992 and August 1997 (Tobón 1999) at a station located at 0°39' S and 72°5' W at 150 m above sea level, at 2.5 km distance from the upland and floodplain plots. Disregarding slight differences between the records from both climate stations, which can be attributed to the different length of the registration period, the climate of this part of the Middle Caquetá Basin is characterized by an annual rainfall of ca. 3100 mm, an average yearly temperature of 25°C and a relative humidity of 87% (Fig. 2-2). This climate is classified as Afí, equatorial superhumid with no dry season (Köppen 1936), i.e. more than 60 mm rainfall in all months and a temperature difference of less than 5°C between the warmest and the coldest month. According to the life zone system of Holdridge (1982; Holdridge et al. 1971) the Middle Caquetá area is classified as humid tropical forest (bh-T).
Figure 2-1. Location of the two permanent plots (M1 = upland plot; M2 = floodplain plot) at Peña Roja, in the middle part of the Caquetá Basin, Colombian Amazonia. The map is derived from Duivenvoorden and Lips (1995).
Both sources (Duivenvoorden and Lips 1995; Tobón 1999) agree that the daily fluctuations in temperature are higher than the yearly fluctuations, and that the range of day and night temperatures is larger in the dry period than in the wet period. High temperatures occur in January and February and low temperatures in June. The latter are associated with a so-called "friaje" or "cold spell" which is a local phenomenon caused by the movement of cold air masses coming from the south of the continent through the Amazon Basin, and whose appearance has also been reported in Brazil (Salati 1985; Tobón 1999). The average monthly maximum temperature at Araracuara ranged from 29.5°C to 32.1°C and the average monthly minimum values from 21.2 °C to 22.6°C (Duivenvoorden and Lips 1995). At Peña Roja the maximum temperature rarely exceeded 35°C and the minimum did not fall below 19°C (Tobón 1999).

Despite the similarity between the mean annual precipitation at Araracuara and Peña Roja, there were a few differences in the yearly distribution pattern. At Araracuara, the average annual rainfall was 3059 mm and showed a unimodal distribution with high values around May, and low values around January (Fig. 2-2; Duivenvoorden and Lips 1995). At Peña Roja the annual average rainfall was 3420 mm and showed a bimodal pattern with a slight decrease in June (Tobón 1999) and between
December and February. The wettest month was September not May, as in Araracuara.

The distribution of rainfall through the year is determined by the trade winds (Domínguez 1987; Botero 1999). Although Araracuara belongs to the Southern Hemisphere its rainfall pattern is typical for that of the Northern Hemisphere, and is furthermore characterized by the absence of a pronounced dry season (Salati 1985). In Colombian Amazonia the pattern of rainfall is controlled by the north-south movement of the belt of intertropical convergence. Most of the rainfall occurs in the afternoon and evening (Tobón 1999; Téllez 2003). At Peña Roja, the wettest year was 1994, and the driest year was 1995. On average it rained on 197 days per year, corresponding to 616 hours of rainfall per year (Tobón 1999; Téllez 2003).

2.3 Hydrology

Peña Roja is located in the catchment of the Caquetá River. This river originates in the Andes and, with a length of 2200 km, it is the largest river in Colombian Amazonia. It is a so-called white-water river, which implies that its water tends to have a whitish color due to suspended clay. The river water has a neutral pH (Duivenvoorden and Lips 1993). The water level of the Caquetá River varies annually according to four seasons: low water, rising water, high water and falling water (Rodríguez 1999). The variation in river water level recorded at several stations along the river ranges from 6.5 m to 8.5 m, with peaks during July-August and low water levels between December-February (Duivenvoorden and Lips 1993; Urrego 1997). In addition to water levels associated to the annual flood cycles, occasionally (once every 3 to 11 years) the river water level rises to exceptional heights. The origin of this phenomenon is unknown, but it has been linked to global climate change, periods of large sunspot activity, or to the influence of El Niño events (van der Hammen and Cleef 1992; Botero 1999).

The floodplain of the Caquetá River is called várzea (Prance 1980; Junk 1984, 1990; Padoch et al. 1999). It is built up by fine sediments which are deposited during overflows (Eden et al. 1982; Hoorn 1990; Duivenvoorden and Lips 1993, 1995). Currently there is no evidence of
gravel transport. The Caquetá River is actively eroding sediments of its fluvial terraces, especially along its southern river bank (Eden et al. 1982).

2.4 Land units

The upland plot (also denominated monitoring plot 1, or M1) is located on a land unit, which was classified as Tertiary Sedimentary Plain by Duivenvoorden and Lips (1993, 1995). This land unit covers between 85-90% of the Colombian Amazon (PRORADAM 1979; Botero 1999). It can be seen as upland or "tierra firme" because it is never flooded by river water (Botero 1999; Duivenvoorden et al. 2001). Locally, uplands are also known as "monte firme" (Spanish) or "baj+hó (Muinane).

The permanent plot is located along the upper slope of a valley (Fig. 2-3) developed in the Tertiary Sedimentary Plain along the left side (downstream) of the Caquetá River, opposite Sumaeta Island (Fig. 2-1), in the Peña Roja community. The plot coordinates are 0°39'31" S, 72°4'38" W. Its altitude is approximately 210 m above sea level.

The soils in the upland plot were classified as Ultisols: Kanhapludults in stable positions and Paleudults in positions with more active erosion (SSS 1987; Alarcón 1990). The soils are deep and show a ABtC profile. In some sectors gravelly sandy materials are found at the top, sometimes with abundant charcoal, which may well be a result of ancient human activity. Textures are sandy loam to clay in the upper horizons, sandy loamy clay in the middle part, and clay or sandy clay in the lower part of the pedon. A detailed soil profile description of a soil pit located just outside the permanent plot (20 m from the northwestern border) was presented by Duivenvoorden and Lips (1993, 1995; plot 125) and is in Appendix 1 (profile 125). At this same location (plot 125) Lips and Duivenvoorden (1996) measured a yearly above-ground fine litter fall of 680 ± 54 g m⁻² y⁻¹ (mean ± one SD) in 1989-1990. The Mean Residence Time of the organic material in the ectorganic horizons was 3.3 y (Duivenvoorden and Lips 1995).
Figure 2-3. Detailed site map of the upland plot (Alarcón 1990; Tropenbos-Colombia 1990). A: relief of the basin showing 2-m isohypses; the values denote the altitude relative to an arbitrary reference point; the total area shown covers 7.2 ha; B: map showing the terrain units and the location of the permanent plot; C: cross-sections showing representative soils along the slopes of the U-shaped valley and the V-shaped valley; D: cover and name of the terrain units.
The floodplain plot (also denominated monitoring plot 2, or M2) is located on a sporadically inundated floodplain of the Caquetá River (Duivenvoorden and Lips 1993, 1995). This land unit is characteristically built up by so-called river bank complexes (convex-concave systems of up to 2 m high river banks alternating with depressions, which run more or less parallel to the main channel of the Caquetá River) and poorly drained basins. The plot was established along the right bank of the Caquetá River (downstream) at 250 m distance from the river, and about 2.5 km north of Sumaeta island (Fig. 2-1). The coordinates of the plot are: 0° 37' S, 72°10' W. Its altitude is approximately 155 m above sea level.

The floodplain of the Caquetá River is locally called "rebalse" or "bajo" (Spanish), and "cajahó (Muinane). In principle, the plot is only flooded when the water level of the Caquetá River is exceptionally high. This occurs every 9-11 years (according to local indigenous informants). Such events are known as "conejerías". Between May and July 1989 the water level reached up to about 2 m above the average surface level of the plot. Each year, between May and July, the concave parts of the plot (Fig. 2-4) become inundated by rain water for about one month. This inundation usually starts in a depression in the eastern part of the plot, which carries water only during the rainiest time of year. For example, during June-July 1990, some parts of the plot were covered by standing water, at a depth of less than 1 m for one month. Due to the low frequency of flooding by the Caquetá River, and the inundation of the lower parts by rainwater, the forest in the floodplain plot can be seen as intermediate between a seasonal várzea and a swamp (sensu Prance 1980). However, in this dissertation the terms várzea and floodplain forest are used, in line with other studies in the area (Urrego 1991). Given its transitional nature and the relatively low influence of flooding by river water, we suggest caution when comparing the results presented here with those of typical Amazonian várzea.

The soil forming processes in the floodplain plot are highly influenced by the continuous supply of organic material from the vegetation and the periodic deposition of sediments during river floods. The fluctuations of the water table induces the alternating reduction and oxidation of the soil pedon. Evidence for this are the gray, olive-green and orange mottles, which occur especially in the soils of the basins and at larger depth in the soils of the convex river banks. Soils were classified as Typic Tropaquente,
Typic and Aquic Dystropept (SSS 1987; Ordóñez 1990). Duivenvoorden and Lips (1993, 1995) described a soil pit in the plot (Appendix 1, profile 126). In the forest directly surrounding this pit they measured a yearly above-ground fine litter fall of $1070 \pm 132 \text{ g m}^{-2} \text{ y}^{-1}$ (mean ± one SD) in 1989-1990 (Lips and Duivenvoorden 1996). The organic material in the ectorganic horizons had a Mean Residence Time of only 1.0 y (Duivenvoorden and Lips 1995).

2.5 Plot location, plot size and sampling set-up

The position of the plots within each land unit was selected such as to ensure that the terrain characteristics regarding relief were similar. Because slopes were hardly developed in the floodplain unit, the upland plot was established at the summit and upper slope positions to minimize the slope (Fig. 2-3). Both plots were set up in forests that lacked any sign of recent human activities. Also in the buffer zones of 100 to 300 m around the plots (Phillips and Baker 2002; Vallejo et al. 2005), no signs of human activities were present.

The conspicuous presence of charcoal in the soils of the upland plot (Alarcón 1990) and the remains of pottery found in nearby fluvial terraces of the Caquetá River (Mora et al. 1991; Mora 2003) demonstrate the ancient human occupation and associated change of the forest cover at the monitoring sites. However, at the time of the establishment of the plots the forests did not show any evidence of recent human interventions. This was also concluded from the presence in the forests of large trees with highly valuable timber, as *Cedrela odorata* (Meliaceae, red cedar) in the floodplain forest and *Mezilaurus itauba* (Lauraceae, Itaúba) in the upland forest.

At the start, in 1989 (Table 2-1) one square 1-ha plot was installed at the upland site (part I in Fig. 2-5). Permanent plots of 1 ha have traditionally been the standard unit of sample area in tropical moist forest inventories, facilitating comparison and also yielding an optimal ratio area/perimeter (Synnott 1979, 1991; Jonkers 1987; Alder and Synnott 1992; Dallmeier 1992). However, on the basis of analyses (not shown) of the first data about the forest diversity using Hill's family of curves (Pielou 1975; Magurran 1988; Krebs 1989) the plot size was increased to 1.8 ha (Londoño and Alvarez 1991). To enlarge the original upland plot of 100 x
100 m, a strip of 20 m wide was added first (part II in Fig. 2-5). At a later stage an extra strip of 50 x 120 m (part III in Fig. 2-5) was established to obtain the final plot of 120 x 150 m (1.8 ha). One year later, in October 1990 (Table 2.1), an equivalent plot of 120 x 150 m (1.8 ha) was established in floodplain forest, with identical parts I, II and III (Fig 2.5).

The plot inventories included all vascular plant individuals that were entirely or partially rooted (i.e. with trunks attached to the soil) inside the plots. Plants rooting precisely on the plot boundaries were included, even if the aerial parts were outside the plot boundaries. The sampling intensity was inversely proportional to the abundance of individuals per size class. Large individuals (DBH ≥ 10 cm; DBH is diameter at 130 cm) were sampled in the entire plot, while the smaller plants were only sampled in a part (Fig. 2-5). The area of the subplots differed per size class (Dubois 1980; Matteucci and Colma 1982; Jonkers 1987; Campbell et al. 2002; Oldeman et al. 2006). Large individuals were sampled in 10 x 10 m subplots, intermediate sized shrubs, lianas and small trees in 5 x 5 m subplots, and small plants (mostly herbs and seedlings) in 2 x 2 m subplots (Table 2-2).

To minimise damage to the plants, the inventory was done in the following sequence: a) demarcation of plots and subplots by setting up the grid of 10 x 10 m; b) inventory of size class C4 (Table 2-2); c) inventory of C1; d) inventory of plants of size classes C2 and C3; and e) measurement of additional variables.

Table 2-1. Installment and census dates of the permanent plots.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Date</th>
<th>Days</th>
<th>Months</th>
<th>Years</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Upland</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>establishment</td>
<td>September 01 1989</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>first measurement</td>
<td>September 01 1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>establishment</td>
<td>September 01 1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>second measurement</td>
<td>December 31 1993</td>
<td>1200</td>
<td>40</td>
<td>3.3</td>
</tr>
<tr>
<td>third measurement</td>
<td>December 31 1997</td>
<td>1440</td>
<td>48</td>
<td>4.0</td>
</tr>
<tr>
<td>fourth measurement</td>
<td>March 31 1999</td>
<td>450</td>
<td>15</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>Floodplain</strong></td>
<td>October 01 1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>establishment</td>
<td>October 01 1990</td>
<td></td>
<td></td>
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<tr>
<td>first measurement</td>
<td>January 31 1994</td>
<td>1200</td>
<td>40</td>
<td>3.3</td>
</tr>
<tr>
<td>second measurement</td>
<td>April 30 1999</td>
<td>1890</td>
<td>63</td>
<td>5.3</td>
</tr>
</tbody>
</table>

*a only 1 ha; b additional 0.8 ha; c only trunk mortality and recruitment
Figure 2-4. Detailed map of the floodplain plot (M2) (Ordóñez 1990; Tropenbos-Colombia 1990; Londoño 1993). A: map showing the terrain units and the location of the permanent plot; the total area shown covers 7.2 ha; B: cross-section, indicating the representative soils and drainage; C: cover and name of the terrain units.
Figure 2-5. Design of the 1.8-ha permanent plots. The roman values I, II, and III indicate the different stages of plot establishment (see text). A: general design; B: design and coding of subplots used to sample the different size classes; C: sampling area for DBH ≥ 10 cm (the largest size class C1); D: sampling area for plants with DBH < 10 cm and DBH ≥ 5 cm (size class C2); E: sampling area for plants with DBH < 5 cm and Ht ≥ 3 m (size class C3); F: sampling area for plants with Ht < 3 m (size class C4). Size classes are defined in Table 2-2.
These variables were measured (or subsequently calculated) using standard methods (Synnott 1979; Caillez 1980; Synnott 1991; Philip 1994; Lema 1995, 2002) and included density (number of individuals), family (Mabberley 1990), genus and species identification, trunk diameter (DBH in cm) height (Ht in m, measured using a Blume-Leiss type hypsometer), crown diameter (in m), biomass (in kg of dry above-ground mass), mortality, survival, recruitment, and tree growth (quantified through diameter and biomass increase).

Table 2-2. Sampling intensity per size class. DBH = DBH is diameter at 130 cm above the soil surface; Ht = plant height. Sampling intensity is the proportion relative to 1.8 ha.

<table>
<thead>
<tr>
<th>Class</th>
<th>Plant size</th>
<th>Subplot size (m)</th>
<th>Subplots</th>
<th>Area (ha)</th>
<th>Sampling intensity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>DBH ≥ 10 cm</td>
<td>10 x 10</td>
<td>180</td>
<td>1.8</td>
<td>100</td>
</tr>
<tr>
<td>C2</td>
<td>DBH ≥ 5 cm and DBH &lt; 10 cm</td>
<td>5 x 5</td>
<td>360</td>
<td>0.9</td>
<td>50</td>
</tr>
<tr>
<td>C3</td>
<td>Ht &gt; 3 m, DBH &lt; 5 cm</td>
<td>5 x 5</td>
<td>120</td>
<td>0.3</td>
<td>16.7</td>
</tr>
<tr>
<td>C4</td>
<td>Ht ≥ 0.5 m, Ht ≤ 3 m</td>
<td>2 x 2</td>
<td>300</td>
<td>0.12</td>
<td>6.7</td>
</tr>
</tbody>
</table>