Tree Species and Tree Ring Characteristics of a Riparian Forest in La Macarena, Upper Colombian Amazon

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ABSTRACT

The characteristics of tree species in a riverside forest were investigated from forest inventory and tree ring analysis of stem transection in three quadrats (100 m² each) along the Duda River in Macarena National Park, Colombia. As the distance from the river channel became longer, the number of individual trees decreased from 103 to 45 (/100 m²), while the canopy height increased from 10 m to 20 m, the diameter at breast height (DBH) increased from 10 cm to 25 cm, and the summation of (DBH)^2 also increased from 3.9 m^3 to 11.62 m^3. Cecropia membranacea was widespread in all the quadrats. This species has the characteristic of fast thickening growth in the early stages but the cycle between establishment and death is shorter than 10 years even in a landside quadrat. Because the vessel diameter is larger than 250 μm, however, it is estimated to be one of the first tree species to be established in a riverbank. Ficus insipida and Piptadenia flavas are believed to be canopy species because they have a large vessel diameter and their growth rate is steady. On the other hand, species with a small vessel diameter such as Guarea guidonia and Inga bomplandiana mainly have thickening growth rather than extension growth and remain as the medium and shrub species.

Key words: riparian forest / tree ring / vessel / Cecropia membranacea / Colombia

In the Amazon where the topographic slope is gentle, rivers sometimes meander and the river water which pours over the channel in the upper course during the rainy season covers both sides with a 1-2 months lag (Sternberg, 1998). In the Amazon Basin, in particular, the hinterlands over a few tens of kilometers are inundated up to several meters in depth during March to August (Junk, 1997). Some species have evolved themselves by developing aerial roots, buttress roots, stilt roots in order to adjust to the soft ground and the long-term non-oxygen condition of rhizosphere (Ogawa et al., 1984, Worbes et al., 1992, Worbes, 1997).

In the upper Amazon near the Andes Mountain Range, on the other hand, the river channels are narrow and are suddenly inundated by the north-south revolution of the intertropical convergence zone (ITCZ). The floods sometimes bring about the change of river course. La Macarena of Colombia, which is the focus of this study, is a typical example of such a region. Although the dry season occurs during December to March and August to September, when the convergence zone shifts to the southern hemisphere, the rainy season continues in other months, and the Duda River between Oriental Mountain Range and Macarena Mountains, erodes the riverbank and pushes away trees at the channel (Hara et al., 1999). However, it is not always eroded. When the flood is over, the debris is
deposited. The meandering of rivers brings about not only erosion but also sedimentation.

The vegetation of riparian forests of Duda River has been reported. Hirabuki (1990) described changes of dominant species from riverside to landside of La Macarena, Hirabuki et al. (1991) examined the development of organic matter in sedimentary soils in the riverside, Takehara & Hirabuki (1991) investigated the establishment of pioneer perennial species in a newly deposited riverbank, and Hara et al. (1999) compared in detail the relationship between the horizontal distance from the river channel and the biodiversity/biomass in a riparian forest. However, the growth chronology and wood anatomical characteristics of tree species have not yet been described. The fact that there are a few dominant species, even in the same riverside with an extent of only 250 m, suggests that each species has its own growth strategy. Therefore, this study will report new findings from tree rings of flood-induced forest in the upper Colombian Amazon.

**STUDY AREA AND METHODS**

**Study Area**

The study site, Puerto Chamusa of Centro de Investigaciones Ecologicas de La Macarena (CIEM), is located in 2°40’N, 74°10’W and the altitude is about 350 m (Fig.1). This area is in the drainage basin of Duda River flowing between the Oriental Mountain Range and Macarena Mountains. The river is a tributary of the Orinoco River, but according to the geographical classification of Colombia, the Macarena Area belongs to an area overlapping the Andes, Orinoco and Amazon (Bibliografica Internacional, 1998). Therefore, the area has an intermediate climatic condition among the three regions; annual precipitation: 2,623 mm, maximum and minimum temperature: 28.9°C and 20.9°C (Hara et al., 1999). The rainy season (April to July, October to November) and dry seasons (December to March, August to September) arrive alternately due to seasonal revolution of ITCZ. The rainy season during April to July frequently brings about flooding from severe rainfall of over 400 mm a month, while in the dry season, the monthly rainfall is less than 50 mm and trees shed their leaves because of water stress (Kimura et al., 1994).

**Methods**

Fieldwork was carried out in a riparian forest in November, 1998 (Fig.1). Quadrat S1 was set up at a place 50 m from the river channel, S2 was set up at a place 120 m from S1, and S3 was set up 60 m in the interior of S2. All quadrats were equally 100 m². The forest inventory (counting the number of individual trees of each species, measurements of tree height and diameter at breast height, DBH) was carried out in each quadrat. Hirabuki (1990) reported that there had been a riparian forest in S3 before the flood of 1986. Tree stems of representative species were obtained at the height of 1 m by a saw or an increment borer in the vicinity of each quadrat (Table 1). Three species were obtained from both S1 and S2, and seven species were obtained from S3. They were taken to a laboratory and were polished by sandpaper attached to a grinder (Nichika, RG-5) after mounting the cores in a rectangular piece of wood (25×25 mm) with a ditch of 5 mm width and 5 mm depth. The mesh #100 was used first, #400 was used next, and #800 was used for the finish. Both surfaces of tree disks were polished in the same manner. The samples were used to measure the tree ring width by a X-Y counter (Nikon, SC-112) connected to a measure scope (Nikon, MM-22) and to investigate the vessel parameters with image analysis software (Mitani, Mac Scope
Fig. 1. Location of research quadrats. Dotted area: riparian forest.

Table 1. Details of tree disks (D) and cores (C).

<table>
<thead>
<tr>
<th>Species</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>Disk/Core</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cecropia membranacea</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>D</td>
</tr>
<tr>
<td>Cecropia membranacea</td>
<td>0</td>
<td>24</td>
<td>27</td>
<td>C</td>
</tr>
<tr>
<td>Guarea guidonia</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>D</td>
</tr>
<tr>
<td>Guarea guidonia</td>
<td>0</td>
<td>12</td>
<td>18</td>
<td>C</td>
</tr>
<tr>
<td>Inga bomplandiana</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>D</td>
</tr>
<tr>
<td>Ficus insipida</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>C</td>
</tr>
<tr>
<td>Piptadeniaflava</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>C</td>
</tr>
<tr>
<td>Spondias monbrii</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>C</td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>C</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>13</td>
<td>39</td>
<td>63</td>
<td>115</td>
</tr>
</tbody>
</table>

Ver.2.5) after inputting the images from a CCD camera (Tokyo Electronics, CS5510).

**RESULTS**

The number of living trees of over 2.5 cm in DBH was 108 in S1, 58 in S2 and 45 in S3. Likewise, the number of dead trees was 10, 5 and 21, respectively. In S1 and S2, *Cecropia membranacea* (Moraceae, local name: Yarumo), *Guarea guidonia* (Meliaceae, Bilibili) and *Inga bomplandiana* (Leg. Mimosoideae, Guamo) were dominant. In particular, numbers of *C. membranacea* were predominant (S1: 83, S2: 35), but the species had a large number of dead individuals as well. As non-arboreal
species, *Gyneryium sagittatum* (Poaceae, Pindo) with the height of about 2 m and *Heliconia* spp. (Musaceae, Platanillo) with the height of 1.5 m were found. The number of living *G. sagittatum* was 39 and the dead *G. sagittatum* was 30. All of *Heliconia* spp. were living individuals and the number was 10. Both sites were covered with herbaceous species up to 30 to 50 cm, but there were no trees or herbs in places topographically lower than the neighborhood. Also, no herbs were found near *Heliconia* spp. In S3, the number of tree species increased, such as *Ficus insipida* (Moraceae, Higueron, the number of individuals: 2) and *Piptadenia flava* (Leg. Mimosoideae, Dormiron, 1), while the relative percentage of *C. membranacea* decreased (S1: 81%, S2: 60%, S3: 40%). *Spondias cf. mombim* (Anacardiaceae, Jobo), *Bursera simaruba* (Burseraceae, Resbalamono) and *Trichanthera gigantea* (Acanthaceae, Nacedero) were also identified outside the quadrat. *G. sagittatum* disappeared
in S3 but Heliconia spp. had a large number (70).

When counting the number of tree rings of 115 stems obtained near each quadrat, the tree age class of 1-5 years was 77% and that of 6-10 years was 23% in S1, while the class of 1-5 years was 8%, that of 6-10 years was 13% and that of 11-15 years was 13% in S2. In S3, however, there were 4 individuals in the class of 16-20 years (8%) and there were 2 individuals even in the class of 21-25 years (4%). This means the forest age of S3 is older than 20 years.

Figure 2 shows the tree height, DBH and (DBH)²H classes of each quadrat. The class of 5-10 m was dominated by C. membranacea in S1, while the difference between C. membranacea and other species was reduced in S2, and there were species which reached 20 m in S3 such as F. insipida and P. flava. However, I. bomplandiana and G. guidonia remained in the medium and shrub layers and did not reach the forest canopy. The DBH also became larger as the distance from the river channel was farther, but most of G. guidonia, which has relatively faster thickening growth than extension growth, appeared in the upper class of S3. The summation of (DBH)²H had a tendency to satisfactorily increase such as 1.39 m³ in S1, 5.79 m³ in S2 and 11.62 m³ in S3.

DISCUSSION

Thickening Growth of Each Species

Trees in this region form tree rings (growth rings) because the cambial activity slows down due to water stress in the dry season. When comparing the number of tree rings of stems obtained near S1, C. membranacea was 5.50 years (SD: ± 0.96), while that of G. guidonia was 4.75 ± 0.43 and I. bomplandiana was 4.33 ± 0.47. This result leads us to estimate that C. membranacea was established first, and it coincides with previous results (Hirabuki, 1990, Hirabuki et al., 1991, Haras et al., 1999). In S2, however, the tree age of C. membranacea (7.08 ± 1.25) is nearly equal to that of I. bomplandiana (7.67 ± 1.25), and it was smaller than G. guidonia (10.17 ± 1.40). The difference extended further in S3; the tree age of G. guidonia was 14.35 ± 3.25, while C. membranacea was 9.44 ± 2.22, F. insipida was 17.0 ± 2.89 and P. flava was 19.2 ± 3.70. This is not inconsistent with the fact that the S3 had been a riverbank before the flood of 1986, and P. flava had been established before the flood. However, the number of C. membranacea established before 1986 is only 3 among 27 individuals in S3, which contradicts the commonly accepted theory that C. membranacea is a pioneer species. Rodrigues (1989) described also that the leaves and stems are eaten from the ants of Azteca, and C. membranacea wither and die due to the insect attack. In fact, most of dead individuals were C. membranacea in every quadrat. Therefore, it is believed that most C. membranacea obtained near S3 are the second descendants of those that were established first.

Because C. membranacea has a large pith cavity in the central part of the stem, it looks bigger than the original when the DBH is measured from the outside. But when making comparisons from the actual thickening growth, the length of C. membranacea is 75.1 mm (SD: ± 21.5) in S3. It is almost equal to G. guidonia (77.3 ± 22.0) and is smaller than F. insipida (114.0 ± 23.2) and P. flava (106.5 ± 12.9). Then, the cumulative tree ring width was compared among representative species obtained near S3 (Fig.3). The number of tree rings taken on average becomes smaller in every species because the tree age is different among the individual trees, but C. membranacea has a large gradient of cumulative ring width and a fast initial thickening growth in all the sites. I. bomplandiana also
Fig. 3. Interannual variation of cumulative ring width in each quadrat. CM: *Cecropia membranacea*, GG: *Guarea guidonia*, IB: *Inga bomplandiana*, FI: *Ficus insipida*, PF: *Piptadenia flava*.

Fig. 4. Interannual variation of growth rate of tree rings obtained near S3. CM: *Cecropia membranacea*, GG: *Guarea guidonia*, IB: *Inga bomplandiana*, FI: *Ficus insipida*, PF: *Piptadenia flava*.
shows the same trend. But the gradient slows down to a similar level to the other species after the abrupt initial growth. This initial growth is clearer when compared by the growth rate, which is defined by the percentage of ring width in a given year of the cumulative ring width up to a year before (Ohsumi, 1987). Figure 4 is the interannual variation of growth rate of 5 species. The initial growth rate of *C. membranacea* and *I. bomplandiana* is prominent, but it drastically decreases after a couple of years. Crawford (1992) explains that juvenile individuals of Cecropiaceae have a fast growth in the initial stage in the middle course of the Amazon because they decay quickly if they do not reach a certain height with no inundation. On the other hand, *G. guidonia, F. insipida* and *P. flava* have an almost constant thickening growth and no change is found in the annual variation in growth rate. These findings show that *C. membranacea* establishes itself first, but the tree age is shorter than
that of other species because it is likely to be eaten by ants and in consequence it maintains the species by succeeding quickly to the next generation.

**Vessel Parameters and Extension Growth**

The extension growth of S3 seems to be satisfactory because there are some individuals like *F. insipida* and *P. flavum* that reach the forest canopy of about 20 m. It is indispensable for the extension growth of plants that vessels absorb soil water up to the growth point, and it is well known that the amount of water which is pumped up through vessels has a close relation to the diameter of vessels. Zimmermann & Brown (1971) explained that the amount of fluid that flows in a cylinder in a unit time is proportional to the fourth power of the diameter. Therefore, the vessel parameters were investigated by an image analysis.

Figure 5 shows the vessels of stem transections taken by a magnitude of 100. They are all the samples obtained near S3. It is common that the distribution pattern of vessels is the diffused arrangement, a few vessels are united (pore multiple), and the fiber and ray parenchyma are clearly found. However, the axial parenchyma is different among species. Regarding *C. membranacea* and *I. bomplandiana*, vessels are enclosed by the vasicentric parenchyma, one type of the paratracheal parenchyma, and a few vessels are enclosed by the confluent parenchyma in the cases of *G. guidonia* and *P. flavum*. In the case of *F. insipida*, the parenchyma is independent from vessel elements and is distributed in a tangential direction (banded apotracheal parenchyma, Shimaji et al., 1976). *C. membranacea* and *I. bomplandiana* have large fibers, and the radial elements are also wide, so that individual cells of ray parenchyma are easily identified in the former species.

The diameter of vessels formed in 1998 was compared (Fig. 6). It exceeded 250 μm in three species (*C. membranacea*, *F. insipida* and *P. flavum*), but was far smaller in *G. guidonia* and *I. bomplandiana*. Tsuchiya et al. (2001) explained from fieldwork about the development of strata of secondary forests in the Brazilian Amazon that the vessel diameter of canopy species was large, while that of species remaining near the forest floor was small. Similar results were confirmed by
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土谷彰男, 小林幹夫, 伊津穂生 コロンビアアマゾン上流部, マカレナ地域における河畔林の樹種と年輪特性

コロンビア、マカレナ国立公園のドゥダ川沿いの河畔林に3箇所の方形区（100 m²）を設定し、每木調査と樹幹横断面の年輪解析から代表種の特性を調べた。河岸からの距離が長くなるにつれて個体数は103から45へと減少したが、樹高は10 m以下から20 mへ、胸高直径（DBH）は10 cm以下から25 cmへ、方形区あたりのDBH合計値は1.39 m³から1.16 m³へと変化した。年輪数から推定した林齢は河岸では10年以下であったが内陸側では25年程度であった。総じて先駆種のCecropia membranaceaが優占していた。この種は初期肥大成長は他種を上回るもの、成長と枯死のサイクルが短く、内陸側でも平均樹齢は10年以下であった。しかし、導管直徳が250 μmを上回ることから短期間に果冠に達する早生種であると推察される。Ficus insipidaやPiptadenia flavaも大径の導管をもつ果冠種であるが、成長率の安定したグループである。一方、導管径の小さいGuarea guidoniaとInga bomplandianaは林内の中下層にとどまり、上長成長よりも肥大成長が中心であると考えられる。