Stand structure and commercial volume of secondary forests in Paraguay and Costa Rica: implications for management options

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SUMMARY

Stand development of secondary forests (established after clearing for agriculture) was studied and compared with primary forest in Paraguay and Costa Rica, focusing on commercial species. Accumulation of bole volume was markedly more rapid in the wetter (Costa Rica) than the drier site (Paraguay). However, the more fertile soils in Costa Rica compared to Paraguay may contribute to a faster development of this stand parameter. The proportion of commercial species contributed by bole volume increased with successional age. In young secondary forests, commercial species at sapling stage were mainly represented by sprout-established individuals, while the proportion of vegetative regeneration declined in more advanced successional stages. Management options and major legal shortcomings are discussed.

Keywords: legal incentives, silvicultural treatments, succession, vegetative regeneration.

INTRODUCTION

In the neotropics, unsustainable agricultural systems are being increasingly replaced by secondary forests, amounting to an estimated area of 165 M ha by 1993 (Weaver 1995). In Costa Rica, one of the countries experiencing a rapid increase of this forest type over the last two decades, secondary forests already cover more than twice the area of forest legally available for production (Fedlmeier 1996). In his review on the management potential of neotropical secondary forest in the humid lowland zone, Finegan (1992) concludes that this forest type has, in general, a high density of commercial species, providing that previous land use was light and seed sources are available nearby. Other studies also document a considerable stocking of commercial species in secondary forests (e.g. Weaver and Birdsey 1986, Morera 1998) and its increasing proportion with successional age (e.g. de Oliveira and Silva 1995, Gomide et al. 1998). However, little is known about the spatial variability and the contribution of sprouts to the commercial stock. Both factors influence management options in secondary forests. Most information on commercial stocking refers to secondary forest in the humid zone that experience only short dry periods or none at all. Also, the effects of soil fertility on successional processes have only been studied in a few cases (e.g. Moran et al. 2000).

In this paper we investigate to what extent both climatic and soil conditions influence the development of commercial stock in secondary forests, using data sets from the subtropical part of Paraguay and the humid Atlantic lowlands of Costa Rica. Both sites are similar in respect to their light land use prior to farm abandonment. We looked at two points in particular. Firstly, the proportion of commercial species in size classes, bole volume, basal area, and sapling density and the spatial variation of these parameters, and secondly, we asked about the role of vegetative regeneration in commercial species. We compared results with primary forests in both sites. Major findings are used to discuss potential management options in secondary forests.

MATERIAL AND METHODS

Study sites

The research in Paraguay was conducted in the District of Choré (24° 06', - 17° 56', 22° 34', W, 80° - 230 m elevation), Department of San Pedro, in the eastern region of the country. Average annual rainfall is 1300 mm and highly seasonal; monthly precipitation from May through August averages < 60 mm. Average annual
temperature is 22.4 °C. The forests of the study area are classified as 'Subtropical, deciduous and mesophytic forests' which formerly covered vast areas in southeastern Brazil, northeastern Argentina, and eastern Paraguay (Hueck 1966). Deeply weathered Oxisols with a low proportion of clay (< 10%) are the predominant soil types in the study area (Olivéira and Burgos 1995).

The study in Costa Rica was undertaken at Boca Tapada (11°05'N, 84°59'W, 50–80 m elevation), Region Hueta Norte, located near the San Juan river which borders to Nicaragua. Mean annual rainfall is 3100 mm with a drier period from February to April (monthly precipitation ~ 75 mm). Mean annual temperature is 26 °C (Herrera 1985). The natural vegetation is classified as 'Tropical wet forest' (sensu Holdridge et al. 1975). Soils are mainly Inceptisols with a clay content of > 60%.

Land use history

In Choré, conversion of pristine forests into agricultural land began in the late 1960s through a colonization programme of the government. Landless farmers in the early days received 10–20 ha, while increasing land shortage in the 1980s led to reducing lots to 3–10 ha. In general, a three years period of cash crop cultivation (tobacco in the first year and cotton in the subsequent two years) follows land clearing. The fallow period ranges from 3–15 years. Fallow vegetation intermixed with primary forests accounted for some 30% of the total land area at the time of this study (1988).

The area around Boca Tapada was colonized in the second half of the last century. The land use pattern is dominated by extensively managed pasture (Montagnini 1994). Landholdings in the study area have an average size of 50 ha (M. Solís, pers. comm.). Many pastures are abandoned after some years because of declining productivity. The forest cover (both secondary and primary forest) in Boca Tapada is estimated at 70% of the total land area.

Site selection

In both sites a chronosequence of young to older secondary forests was selected by interviewing farmers. In Paraguay, young secondary forests were 2-, 3-, 4- and 5-years old, while the older stands had an age of 10 and 15 years. In Costa Rica, selected sites were 2.5-, 5.5-, 9-, 12-, 18-years old. For comparison, primary forest was sampled in both sites. Land use, as either three years cropping of tobacco and cotton in Paraguay or two to three years pasture use in Costa Rica, was light. Only in the 5.5-year old stand in Costa Rica, where two years of pasture use followed two years of rice cultivation, land use was slightly longer than in other stands. Primary forest was within 100–200 m distance in all cases. Remnant trees were absent in Paraguay, while some residual trees and palms were found in the youngest secondary forests (2.5–9 years old) in Costa Rica.

Data collection

In any successional stand four rectangular plots of 500 m² each were randomly established. In the primary forest, 8 and 7 plots, respectively were laid out in Paraguay and Costa Rica. Trees and palms ≥ 5 cm DBH (diameter at breast height) were measured and identified. In a rectangular strip of 100 m² within each major sampling unit, saplings (Paraguay: 1 – 4.9 cm DBH; Costa Rica: 130 cm height – 4.9 cm DBH) were sampled. In both strata, individuals were categorized as either sprout or seed regeneration. Trees were measured for total height and bole height. Bole volume (BV) was determined by using the formula:

\[ BV = \text{basal area} \times \text{bole height} \times 0.7 \] (form factor)

In the primary forest in Costa Rica sampling was confined to the measurement of DBH and species identification of trees and palms ≥ 5 cm.

Species grouping

Tree species were categorized into the following groups: (1) high to medium commercial value, (2) low or potential commercial value, and (3) non-commercial (henceforth 'commercial', 'potential' and 'non-commercial species'). In Paraguay, this grouping is based on a classification of the Ministerio de Agricultura y Ganadería (1988) and recent information (M. Grulke, pers. comm., 2000). In Costa Rica, species classification is based on an official list of the Forest Service issued in 1991 and an inquiry conducted in saw mills of the region (Fedlmeier 2000). Of 79 species sampled in Paraguay, 23 have commercial value, whereas 27 out of 180 species recorded in Costa Rica fall into this group (see complete list in Appendix 1). In both sites, most large trees are already commercialized, while species with potential value are mainly medium-sized trees with relatively soft wood. In Costa Rica, in contrast to Paraguay, very few species have a high commercial value. Non-commercial species are chiefly small trees and shrubs, and fast-growing pioneer species.

RESULTS

Size-class distribution

In Paraguay, stem density in the lowest size class lost dominance in the older secondary forests, while the size-class distribution of trees in Costa Rica showed a reversed J-shape form throughout the successional sequence (Figure 1, 2). The move away from the negative exponential size class distribution in Costa Rica may be a temporary lack of regeneration due to crown closure. In Costa Rica, stem density in all successional stands and primary forest was, in general, much higher than in
FIGURE 1  Size-class distribution of trees ≥ 5 cm DBH by commercial groups in successional stands (n=4) and primary forest (n = 8) in Paraguay. Mean stem density per size class ± 1SE.
FIGURE 2. Size-class distribution of trees ≥ 5 cm DBH by commercial groups in successional stands (n=4) and primary forest (n = 7) in Costa Rica. Mean stem density per size class ±1SE.
Paraguay. Both findings suggest that the crown area of dominating individuals in Costa Rica is, on average, smaller and more evenly distributed than in Paraguay, and hence allowing more trees to thrive in an individual area.

In both sites, commercial species were erratically distributed among size-classes in the successional stands. In secondary forests in Paraguay, non-commercial species were more common in the different size-classes in absolute and relative terms than in primary forest. In Costa Rica, the number of non-commercial species in the lower size-classes (< 15 cm DBH) of successional stands was higher than in the primary forest, while this group of species showed a higher relative abundance in the latter stand. Palms showed an irregular abundance pattern among stands.

**Bole volume and basal area**

In both sites, bole volume and basal area increased steadily with successional age (Table 1). For both stand parameters, considerably higher values were found in Costa Rica, indicating better growth conditions compared with Paraguay. Also, the basal area of secondary forests in Costa Rica approached faster to the value of the primary forest. In general, the spatial distribution of bole volume in secondary forests in Paraguay was less variable than in Costa Rica. Remnant trees in the latter site are unlikely to be the rationale for the greater spatial variability, because they are missing in the older secondary forests.

In Paraguay, the percentage of commercial species on total bole volume increased as time elapsed from farm abandonment, while the proportion of non-commercial species declined correspondingly. In Costa Rica, by contrast, there was no clear trend which is due to the distinct set of dominant species in the different stands. In the 2.5- and 9-year old secondary forests, potential and non-commercial species, respectively such as *Laetia procera* and *Cecropia insignis* were the most common trees. In the 5.5-year old secondary forests, *Carapa guianensis* and *Tapirira guianensis* as remnant trees of medium commercial value, were beside *Ochroma lagopus* (non-commercial species) and the formerly mentioned species the dominant components. *Vochysia ferruginea*, a commercial species, was predominant in the 12-year old stand. In the oldest secondary forest, *L. procera*, *Cordia bicolor*, *Pentacletra macroloba* and *Simarouba amara*, the last two species with commercial value, had the highest proportion in bole volume. In Paraguay, non-commercial species, particularly *Tremia micrantha* showed only a high percentage in bole volume in the youngest secondary forests. In the older secondary forests, commercial and potential species, respectively, notably *Peltophorum dubium* and *Macarueria minutiflorum*, representing the former and latter group, had the highest individual proportion in bole volume. In the primary forest, *Balfouriodendron riedelianum*, belonging to the species with high commercial value, showed the highest individual proportion in total bole volume. This species was also well-represented by small size individuals in all secondary forests.

**Table 1** Variation of bole volume (m³ ha⁻¹, trees ≥ 5 cm DBH), proportion of individual species groups (1 = 'commercial'; 2 = 'potential'; 3 = 'non-commercial species') on bole volume, and basal area (m² ha⁻¹; percentage of sprouts in parentheses) in secondary regrowth stands of different ages and primary forest in Paraguay and Costa Rica

<table>
<thead>
<tr>
<th></th>
<th>m³ ha⁻¹</th>
<th>% species groups</th>
<th>m³ ha⁻¹</th>
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<tbody>
<tr>
<td></td>
<td>n</td>
<td>range</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean±SD</td>
<td></td>
</tr>
<tr>
<td><strong>Paraguay</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-3-y old</td>
<td>4</td>
<td>0.8 – 5.5</td>
<td>3.2 ± 2.5</td>
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<tr>
<td>4-5-y old</td>
<td>4</td>
<td>14.3 – 24.8</td>
<td>18.7 ± 4.8</td>
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<tr>
<td>10-y old</td>
<td>4</td>
<td>15.6 – 45.2</td>
<td>31.6 ± 13.4</td>
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<tr>
<td>15-y old</td>
<td>4</td>
<td>34.8 – 61.2</td>
<td>48.8 ± 10.8</td>
</tr>
<tr>
<td>Primary forest</td>
<td>8</td>
<td>126.2 – 208.2</td>
<td>161.9 ± 26.4</td>
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<tr>
<td><strong>Costa Rica</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5-y old</td>
<td>4</td>
<td>1.9 – 5.6</td>
<td>4.1 ± 1.7</td>
</tr>
<tr>
<td>5.5-y old</td>
<td>4</td>
<td>20.2 – 80.3</td>
<td>41.4 ± 26.7</td>
</tr>
<tr>
<td>9-y old</td>
<td>4</td>
<td>76.5 – 122.4</td>
<td>90.4 ± 21.7</td>
</tr>
<tr>
<td>12-y old</td>
<td>4</td>
<td>66.8 – 123.9</td>
<td>106.3 ± 26.6</td>
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<tr>
<td>18-y old</td>
<td>4</td>
<td>154.2 – 237.1</td>
<td>182.9 ± 37.9</td>
</tr>
<tr>
<td>Primary forest</td>
<td>7</td>
<td>-</td>
<td>-</td>
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</tbody>
</table>

* no data
In the young secondary forests in Paraguay, commercial species ≥ 5 cm DBH established themselves mainly by sprouting (58%), while vegetative regeneration played only a minor part (< 18%) in more advanced successional stages; in the primary forest, all individuals were seed-established. In Costa Rica, by contrast, the percentage of sprout-established individuals increased along the chronosequence.

**Sapling density**

Mean sapling density of commercial species declined with successional age in Paraguay (Table 2). The increased sapling density in secondary forests compared with the primary forest was, in part, due to sprout-established individuals. In Costa Rica, there was no clear trend. However, similar to the secondary forests in Paraguay, sprout-established individuals were more common than seed-established individuals in the younger secondary forests. The important role of sprout-established individuals in early successional stages in both sites indicates that land use intensity was in fact similar, although the type of land use prior to farm abandonment was different. On average, sapling density of potential species was higher in secondary forests of both sites (Paraguay: \( \bar{x} = 22.5 \) ind./100 m\(^2\); Costa Rica: \( \bar{x} = 25.7 \) ind./100 m\(^2\)) compared to commercial species.

The higher total sapling density in Costa Rica is due to the lower minimum size for measurement of saplings compared to Paraguay. In general, sapling density declined sharply during succession in both sites, indicating crown closure. In Paraguay, commercial species accounted for about one-third of the total sapling density, while this group of species had only a small proportion in Costa Rica. Potentially commercial species showed a higher proportion in the total sapling density in secondary forests in Paraguay (45%) than in Costa Rica (17%).

**DISCUSSION**

The small sample size in both study sites limits the generalization of the results. However, some trends can be picked up to discuss management strategies for the secondary stands sampled.

This study showed that both climatic and soil conditions clearly influence the productivity of secondary forests. Based on interpolation (by dividing mean bole volume by stand age) and excluding the youngest stand in each site, periodic mean annual increment in Paraguay is about 3.5 m\(^3\) ha\(^{-1}\), while the secondary forest stands in Costa Rica show a much faster growth throughout the chronosequence (on average, 9 m\(^3\) ha\(^{-1}\) y\(^{-1}\); remnant trees were excluded) (cf. Table 1). However, in most secondary forest stands species with high or medium commercial value accounted for less than 50% of the total bole volume. Overall, figures in Paraguay correspond to values found in logged-over primary forest (Silva et al. 1995), and young and older secondary forests in Brazil (Gomide et al. 1998, de Oliveira and Silva 1995), whereas the accumulation of commercial volume in Costa Rica is similar to teak plantations of low productivity (cf. Bhat 2000).

### Table 2: Stem density of species with commercial value at sapling stage (Paraguay: 1 - 4.9 cm DBH; Costa Rica: 130 cm ht - 4.9 cm DBH) in 100 m\(^2\) plots, origin of individuals, and total stem density per hectare (in parenthesis, percentage of the aforementioned group of species) in secondary regrowth stands of different ages and primary forest in Paraguay and Costa Rica

<table>
<thead>
<tr>
<th></th>
<th>Saplings/100m(^2)</th>
<th>%</th>
<th>Stems ha(^{-1})</th>
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<tbody>
<tr>
<td></td>
<td>n</td>
<td>range</td>
<td>mean±SD</td>
</tr>
<tr>
<td><strong>Paraguay</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-3-y old</td>
<td>4</td>
<td>10 - 73</td>
<td>34.8 ± 27.0</td>
</tr>
<tr>
<td>4-5-y old</td>
<td>4</td>
<td>8 - 31</td>
<td>19.8 ± 10.2</td>
</tr>
<tr>
<td>10-y old</td>
<td>4</td>
<td>9 - 19</td>
<td>13.5 ± 4.4</td>
</tr>
<tr>
<td>15-y old</td>
<td>4</td>
<td>7 - 21</td>
<td>11.0 ± 6.7</td>
</tr>
<tr>
<td>Primary forest</td>
<td>8</td>
<td>1 - 5</td>
<td>2.8 ± 1.7</td>
</tr>
<tr>
<td><strong>Costa Rica</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5-y old</td>
<td>4</td>
<td>1 - 13</td>
<td>7.3 ± 5.1</td>
</tr>
<tr>
<td>5-5-y old</td>
<td>4</td>
<td>1 - 7</td>
<td>3.0 ± 2.7</td>
</tr>
<tr>
<td>9-y old</td>
<td>4</td>
<td>3 - 14</td>
<td>8.3 ± 5.1</td>
</tr>
<tr>
<td>12-y old</td>
<td>4</td>
<td>1 - 23</td>
<td>11.0 ± 9.6</td>
</tr>
<tr>
<td>18-y old</td>
<td>4</td>
<td>4 - 9</td>
<td>7.3 ± 2.2</td>
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</table>
Fedlmeier (1996) remeasured the plots in Costa Rica one year after establishment and found that in older secondary forests fast volume increment continued, while it declined in young secondary forests. Mean annual diameter increment, however, was higher in the 2.5-year old stand (1.57 cm) than in the 9-, 12- and 18-year old stand (0.35, 0.46 and 0.27 cm, respectively). This reversed trend is both due to the changing species composition, from fast-growing pioneers to generally slower growing successional species, and the higher stem density in older secondary forests (cf. Figure 2). Thus, fast volume increment in more advanced successional stands is distributed over a large number of trees, decreasing the individual diameter increment. To reverse this trend, silvicultural treatments are required.

Timing, selection of potential crop trees, and intensity of interventions are crucial for the economic viability of timber production in secondary forests. Silvicultural treatment in the first stage of arboreal succession, characterized by the light canopy of non-commercial pioneers is not recommendable, because access and locating as well as identifying valuable regeneration is still difficult (cf. Finegan 1992). However, Guazigua (1999) found in a 4.5-y old secondary forest with sufficient commercial stocking that liberated trees of L. protera, T. guianensis and V. ferruginea showed significantly faster diameter increment rates two years after treatment compared to control plots. The dynamic stratification of the canopy in early successional stages however may lead to fast closure, marginalizing the positive effect of treatment after a few years. This holds particularly for the former two species, while V. ferruginea can maintain fast growth for periods of time without any treatment. Moreover, it is questionable whether it makes sense from an economic point of view to liberate low price timber such as L. protera. Silvicultural treatments should be carried out at a stage when increased mortality has subsided and the canopy offers a sufficient pool of individuals with high or medium commercial value. The considerable number of sprout-established commercial species may constitute a technical problem, because we know little about their long-term performance (cf. Hummel 2000). For example, it is not clear whether sprout-established individuals are capable of forming a clear and straight bole and to what extent they are more prone to wind damage than individuals from seed. Thus, treatments may concentrate on individuals emerging from the latter mode of regeneration. The proper time for silvicultural treatments may be earlier in the Paraguay stands (before 10 years of age) than in the Costa Rica stands (at about 15 years of age), because of the prolonged increase in stem density and the low proportion of commercial species in the young secondary forests of the latter site (cf. Figure 2). It remains to be investigated whether early treatments provide a return to forest owners. Silvicultural treatments in a 20-y old secondary forest in Costa Rica with a low proportion of preferred species on the total basal area were not profitable, because trees of log size were missing (Hutchinson 1995). By contrast, in a 40-y old secondary forest, income from sawlogs and firewood harvested by the selective removal of 31 percent of the basal area, exceeded operational costs (Hutchinson 1995); diameter increment rates of selected trees doubled after the considerable reduction in basal area (Hutchinson 1993). The scarce information available suggests that only a bold reduction in basal area in short intervals can produce future harvests of better quality and greater volume in an acceptable timeframe through long-lasting fast growth of commercial species (de Graaf 1986). This suggestion is supported by the simulation of logging scenarios in the secondary forest stands in Paraguay over a period of 300 years where short cutting cycles in 10 year intervals with relatively high extraction rates (up to 20 stems/ha per cycle) provided a higher sustainable timber yield than longer cutting cycles (Kammesheidt et al., submitted).

Management of secondary forests will only be an alternative to other land use systems such as timber plantations if incentives are provided. In Costa Rica, the legal definition of secondary forest by the 'Principle 11' in 1999 was the first step towards the management of this renewable resource (Solís 2000). In Paraguay, by contrast, secondary forests are neither mentioned nor defined by the forest law (Wippel et al. 1997). In recent years, farmers in Costa Rica could receive payments for the environmental services of secondary forests. Funds for protection are given for ten years as maximum (E. Müller, pers. comm.). The 'Principle 11' explicitly mentions that also secondary forest management qualifies for payments of environmental services (Solís 2000). To date, however, no funds have been provided based on this regulation, except on experimental basis (M. Solís, pers. comm.). Funds available to the forestry sector are mainly allocated to reforestation programmes (Araya 1998, Oficina Nacional Forestal 2000).

Subsidizing environmental services of secondary forests, as has been done in Costa Rica, would probably have a more long-lasting effect on the conservation of this forest type if it is linked to management. Due to the generally high commercial value in secondary forests, timber stand improvement (which might include enrichment plantings in areas with relatively low commercial stocking, cf. Table 1, 2) is a promising management option and should receive financial support, particularly in cases where immediate profit is not likely. Moreover, implementing such a policy is the only way to evaluate the ecological and economic viability of secondary forest management in an objective way when compared with plantation forestry.

CONCLUSIONS

Management of secondary forests in countries with fast dwindling primary forest resources such as Paraguay and Costa Rica (cf. Harcourt and Sayer 1996) is the last
opportunity to combine timber production with the conservation of at least part of the original vegetation. Major prerequisites for the implementation of secondary forest management are:

1. The provision of a legal framework of incentives, 
2. Marketability of secondary forests products, and 
3. Accessibility.

These conditions would help reduce the competitive disadvantages of secondary forest management when compared against plantation forestry.

ACKNOWLEDGEMENT

Field work for both studies was funded by Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ). The first author benefited from the discussion with Eva Müller and Manuel Solis (both GTZ-COSEFORMA, Costa Rica) who also organized a field trip to Boca Tapada. The writing of this article was made possible by an earlier draft of this manuscript. We appreciate the comments of three unknown reviewers on an earlier draft of this manuscript.

REFERENCES


DE GRAAF, N.R. 1986 A silvicultural system for natural regeneration of tropical rain forest in Suriname. Agricultural University of Wageningen, the Netherlands.


APPENDIX 1 List of commercial tree species with high (indicated with an asterix) or medium value in Paraguay and Costa Rica

Paraguay

Anadenanthera colubrina *Brenan
Apuleia leiacarpa *Macbride
Astronium fraxinifolium Sch.
Balforoudendron riedelianum *Engl.
Cabralea canjerana Mart.
Cedrela fissilis Vell.
Cordia trichotoma Arrab. ex St.
Chrysophyllum gonocarpum Engl.
Enterolobium contortisiliquum Mor.
Holocarux balancae Hassler
Lonchocarpus muehlbergianus Mor.
Luehea divaricata Mart.
Myrciania rivularis Cambess
Myrocarpus frondosus Allmão *
Ocotea dioxyphylloa Mez.
Parapiptadenia rigidabrenan
Panagonia americana L.
Peltophorum diabium Taub.
Ruprechtia laxiflora Meisn.
Sweeta fructicosa Sprengel *
Tabebuia impetiginosa *Standl.

Costa Rica

Brosimum alicastrum Sw.
Brosimum guianense *Huber ex Ducke
Carapa guianensis Aubl.
Dialium guianense Steud.
Dipteryx panamensis *Pittier
Enterolobium schomburgkii Benth.
Elaeolamna glabrescens (Mart. & Eichl.) Aubrev.
Hieronyma alchorneoides
Minquartia guianensis Aubl. *
Ocotea sp.
Pentaclethra macroloba Kuntze
Pithecellobium macradenium
Pterocarpus hayesi Hemsl.
Qualea paraensis Ducke
Singarouba amara (Engl.) Readl. ex Boas
Sipoea fagia Standley
Symphonia globulifera 1.f.
Tapirira guianensis Aubl.
Terminalia amazonica (J.F. Gmel.) Excell
Tetragastris panamensis Kuntze
Vatairea undellii (Standley) Killip
Virola sebfiera Aubl.
Virola koschyi Warb.
Vitex cooperti Standley
Vochysia alleni Standley & L.O. Williams
Vochysia ferruginea Mart.
