

Plant Phenology in a Lowland Atlantic Tropical Wet Rainforest

A phenology study at Caño Palma Biological Station

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Abstract

This study aimed to understand the influence of the weather and environment on the phenological pattern of trees in a Lowland Atlantic Tropical Wet Rainforest in the Northeast of Costa Rica. Knowing the timing of the phenophases is meaningful so for instance the available food sources for animals are known. Also phenology is a way of understanding the ecosystem dynamics and discovering/documenting what potential effects climate change has on rainforests. During 2013-15, 160 trees in the jungle were observed monthly on flowering, fruiting, leaf flushing and leaf fall. Also since October 2014, 170 trees along the Caño Palma canal were observed twice a month on these phenophases. Trees in general tend to show more flowering, fruiting and leaf flushing in dryer periods. For the leaf fall no distinct pattern was found, which might be explained by the lack of data on this phenophase. Also this study has shown different phenological patterns per species. Some of the species showed a flowering peak in the dry season while others showed flowering in the wet season. For *Pentaclethra macroloba* the influence of the environment on leaf flushing and leaf fall was seen, likely due to the different amounts of light available. This study is going to be continued over the years which is required to better document and understand species-specific phenology and long-term trends and changes in tropical rainforest tree phenology. In addition to continuing data collection in the future, it is important all data is collected by the same observer or people trained by this observer so no data is missing or biased.

1. Introduction

Phenology is the study of the periodicity of recurring growth stages in the life cycles of plants and animals, and the influence that the environment has on these events (Sakai, 2001; Chuine *et al.*, 2007; Adamik *et al.*, 2014). Plant phenology studies are of great importance to understand evolutionary processes, ecosystem dynamics and the effects of climate change (Chuine *et al.*, 2007; Ailene & Wolkovich; Assunção *et al.*, 2014). Vegetation is an important part of an ecosystem, as it provides the net primary productivity necessary to support nearly all other organisms (Behm *et al.*, 2008). A lot of animals are dependent on the production of leaves, fruit or flowers as a food source. Thus the time of the year of fruiting and flowering is important to understand, for example, feeding behavior (Castro *et al.*, 2012). Several abiotic factors such as light (Schaik & Wright, 1994), temperature (Malhi & Wright, 2004) and rainfall (Lewis *et al.*, 2004) are all in flux and can contribute to flower, fruit and leaf production effort (Boesch & Polansky, 2013). To understand the effects of these abiotic factors, the phenophases (flowering, fruiting, leaf flushing and leaf fall) need to be monitored. Research needs to be done for at least several years to get a good image of the phenophases and their environmental correlates. Although it is of great importance, not many phenology studies have been done in tropical rainforests (Han *et al.*, 2013). To properly monitor and preserve the rainforests in the world it is important to understand the changes in the ecosystems and monitor the effect of climate change on trees (Sakai, 2001).

This study focused on the phenology of trees in a Lowland Atlantic Tropical Wet Rainforest in Northeast Costa Rica. The research took place at Caño Palma Biological Station which is owned and operated by the Canadian Organization for Tropical Education and Rainforest Conservation (COTERC). In 2011 a phenology transect was established at Caño Palma Biological Station, and since then data has been collected once a month. This transect is located in the rainforest surrounding the station. To gain a broader understanding of the phenology of the region, a new transect was established along the canal adjacent to the station. This new transect will also shed light on the influence of the environment on the observer, because the canopy along the canal is easier to see than the canopy in the rainforest. The dense palm midstorey in the forest can negatively affect the visibility of flowers, fruits and leaves, which will be demonstrated in the differences between the two transects. There may also be a difference in abiotic factors between the two transects which can influence the phenophases of the trees. With this extra transect and more frequent data collection more phenology data can be generated to monitor growth stages over the years. In this study the phenological data of the last three and a half years of the jungle transect were analyzed. This study also included the setup of the new transect along the canal, and the data collection and analysis of this transect.

2. Methods

2.1 Study area

The station is located in the Caribbean Lowlands of Costa Rica, in the Barra del Colorado Wildlife Refuge, about 200 meters from the Caribbean Sea (Figure 1). The region surrounding the station is classified as a Lowland Atlantic Tropical Wet Rainforest and is composed of monospecific *Manicaria saccifera* swamp in the lower zones and mixed forest in the slightly drier parts (Grant *et al.*, 2010).

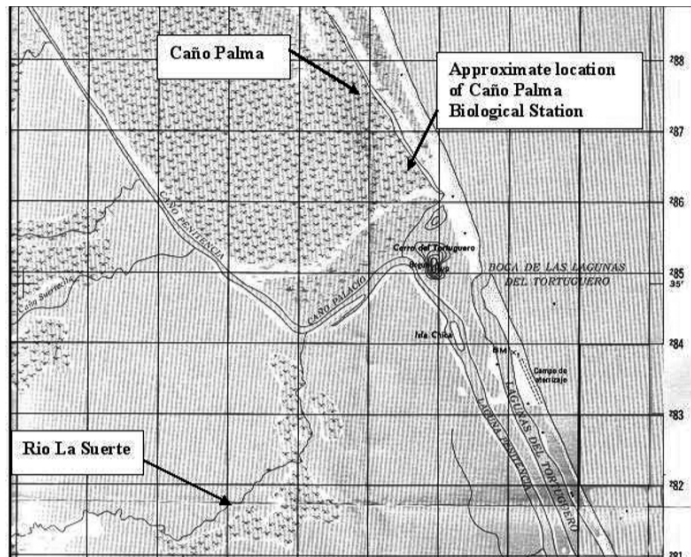


Figure 1 Map showing the approximate location of Caño Palma (Instituto Geográfico de Costa Rica (Servicio Geodesico Interamericano. IGCR Mapa Edición 1. Hoja 3447 I - 1:50,000. N 104081/W 833081)

2.2 Data collection

For the new canal transect a total of 175 trees were tagged with aluminum tags with their identification number on it; 83 south of the station (from the station to the end of the canal) and 92 north of the station. The number of trees was chosen to get a representative sample of the trees along the canal. Trees were selected based on their visibility, so the tag and the canopy could be seen from the canal and on the species of tree so that several different species are included. With the help of ethnobotanist Mario García Quesada, all the trees were identified to species. Twice a month the data was collected from the canal. This time interval was chosen so that all phenophases would likely be seen. Each tree was examined using binoculars and the phenophase noted. This phenology method yields the most data and is most efficient given time and logistical constraints. This method has been used before by González & Origgi (1997), Camacho & Orozco (1998) and Leandro (2013). According to this method any flowering, fruiting, new leaves or dropped leaves are noted with the intensity of each phenophase in percentages of 0, 25, 50, 75 or 100 percent. The intensity of a phenophase is determined by the amount of coverage of the tree, for example: if half of the tree is growing flowers the phenophase for flowering has an intensity of 50%. The data collection will go on for several years and in the end another data analysis will be done, for this study the data until the end of December was used. The forest transect was set up and identified using the same method as the canal transect and the data collection was done in the same way, except that the forest transect was done only once per month. For the canal transect a total of 3 months of data were used for analysis and for the jungle transect a total of 45 months of data were used.

2.3 Data analysis

The goal is to continue this research over many years and collect a big dataset that in the future can be used to detect trends and changes in the phenophases over the years. For this research, data from several years of research in the rainforest was compared. The difference in temporality of phenophases from every year was analyzed. This was done for all trees in general, and per species. With this analysis, changes can be seen between the phenophases of a tree from one year to the other and between different species. The transect on the canal was set up this year, so no data of different years could be used for comparison, so only the three months of the study period were compared with one another. A Friedman analysis is used to compare the phenology data collected from the canal. The three months of data from the canal transect were compared with the same three months of data from the jungle transect.

3. Results

At the start of this study, the forest transect consisted of 157 trees with a total of 37 different groups; 142 trees were identified to species, 6 trees were identified to genus, 8 were identified to family and 1 tree could not be recognized in any way (Appendix Table 1). The canal transect consisted of 176 trees, all of which were identified to species with a total of 21 different species (Appendix Table 2). Because the data was not collected on a regular basis at the beginning of this study the data from 2011 and 2012 were not used for this analysis. The phenophase dropped leaves was not used until January 2014 so for this phase there is only data from one year.

3.1 Jungle transect

For all the species together a peak in flowering was seen every year from February until July and a fruiting peak was seen between June and November (Figure 1a). Also it appears that all trees produce more new leaves from February until May (Figure 1b).

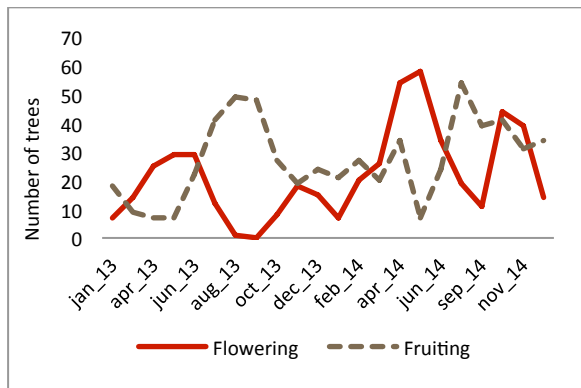


Figure 1a Flowering and fruiting of all trees of the forest transect

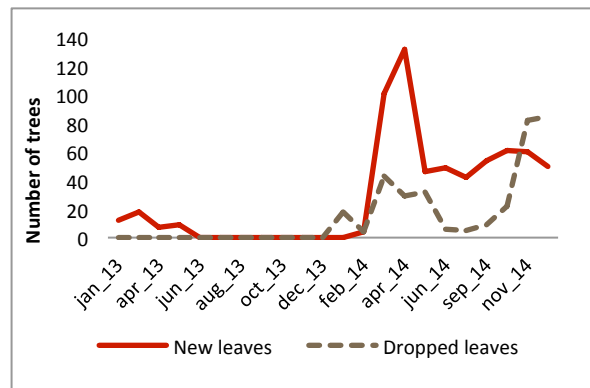


Figure 1b Producing of new leaves and dropping of old leaves of all the trees in the forest transect

In this study the differences between several species in the jungle transect were compared, for which all species with more than 7 individuals on the transect were used. The analyzed species are *Pentaclethra maculoba*, *Vochysia ferruginea*, *Apeiba membranacea*, *Carapa nicaraguensis*, *Malouetia guatemalensis* and *Homalium guianense*. For *Pentaclethra maculoba*, there was a twice annual peak of flowering and the fruiting happened year-round with a decrease around May (Figure 2). The species produced new leaves from September until April, the dropping of leaves did not show a distinct cycle.

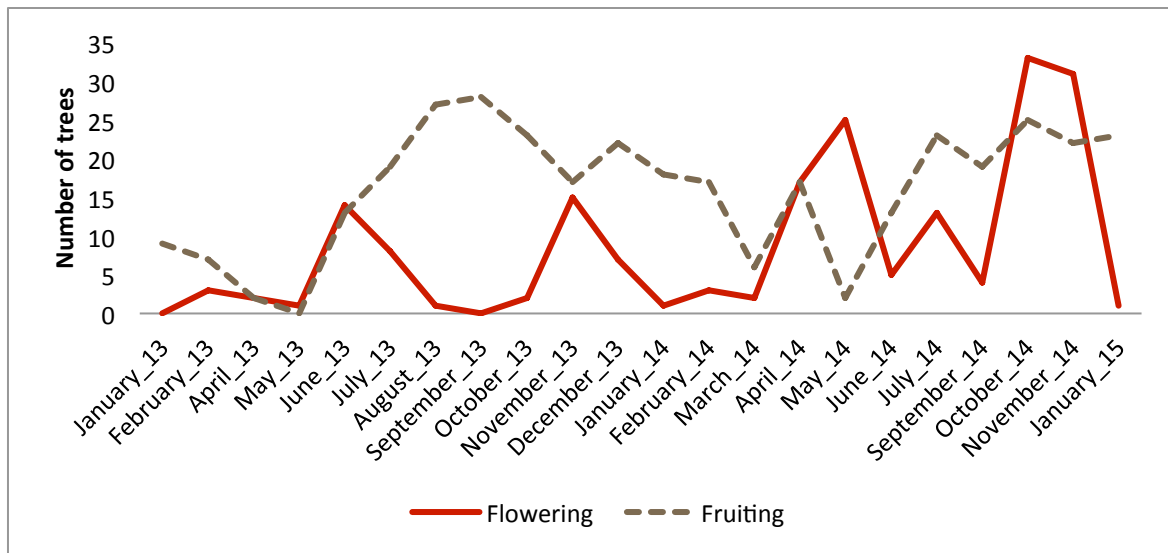


Figure 2 Flowering and fruiting of *Pentaclethra macroleoba*

For *Vochysia ferruginea* a flowering peak is seen every year between March and July and between June and October a fruiting peak can be seen (Figure 3). Between February and September the trees were producing new leaves. The phenophase of leaf fall showed no pattern.

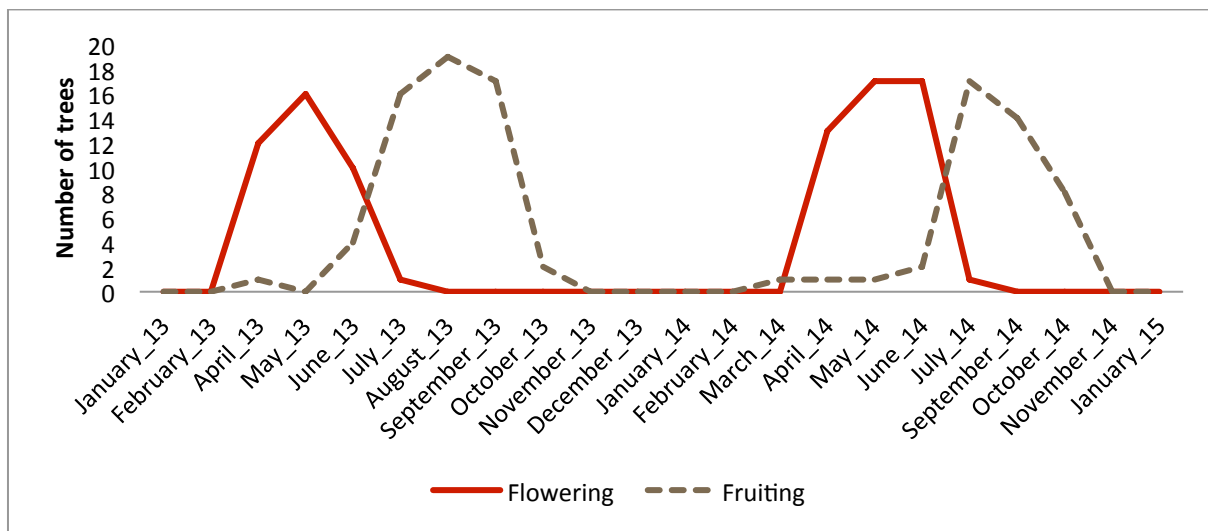


Figure 3 Flowering and fruiting of *Vochysia ferruginea*

Apeiba membranacea showed twice annual flowering, and fruiting from January until June (Figure 4). The trees were producing new leaves between March and October and for the leaf fall no distinct pattern was seen.

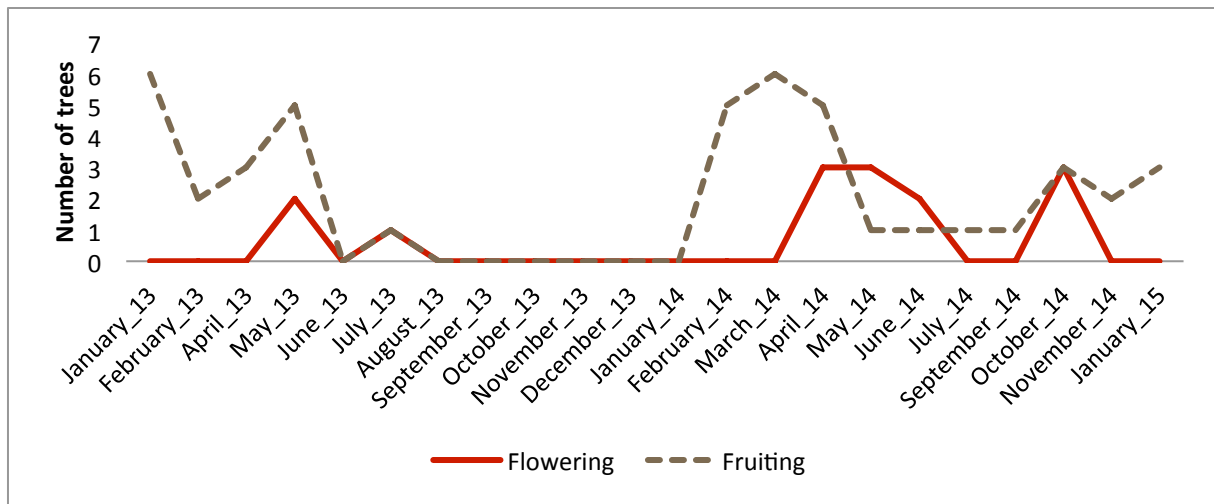


Figure 4 Flowering and fruiting of *Apeiba membranacea*

The *Carapa nicaraguensis* showed twice-annual flowering which shifted over the years. The fruiting appears to increase after the flowering (Figure 5a). New leaves are produced from March until June and in October and November. The leaf fall is ongoing through the year (Figure 5b).

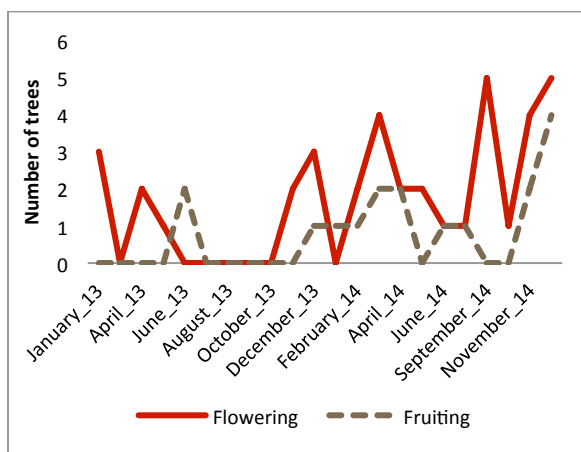


Figure 5a Flowering and fruiting of *Carapa nicaraguensis*

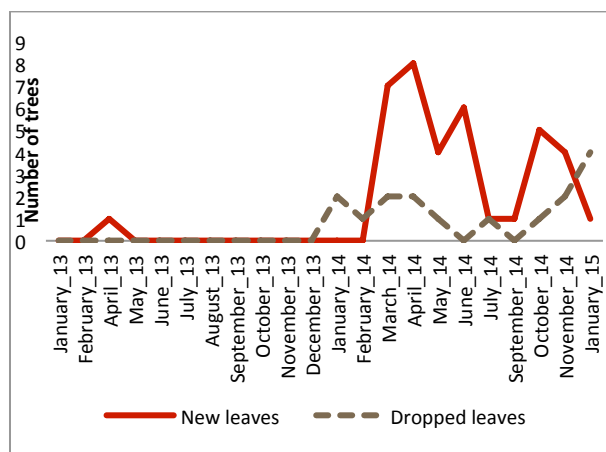


Figure 5b Leaf flushing and leaf fall of *Carapa nicaraguensis*

Flowering on *Malouetia guatemalensis* occurred from February until May and from October until November. Not much fruiting was observed with this species, only small peaks were seen in April and July (Figure 6a). A peak in leaf flushing was seen from March until April. The leaf fall showed several small peaks but did not show a pattern over the years (Figure 6b).

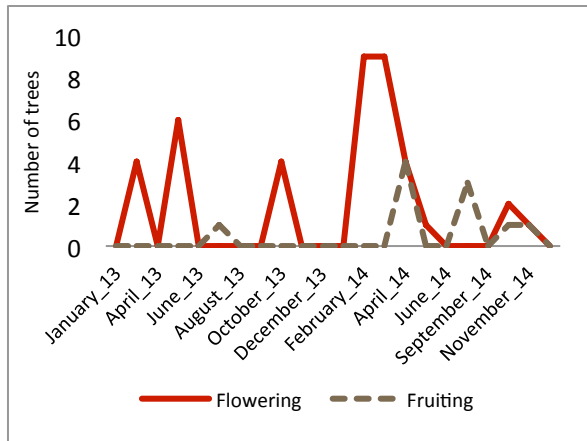


Figure 6a Flowering and fruiting of *Malouetia guatemalensis*

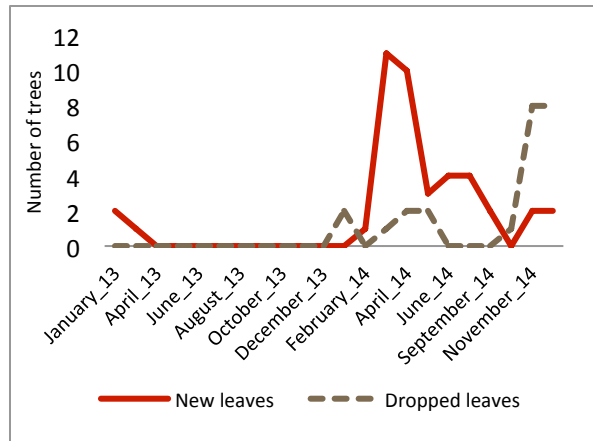


Figure 6b Leaf flushing and leaf fall of *Malouetia guatemalensis*

Homalium guianense showed flowering in December and January and also later in the year around April and May. Fruiting was only seen in the end of 2013 and in 2014, with a peak from February until April (Figure 7a). New leaves were mainly produced in 2014 in March and April and from November until January. Leaf fall occurred from September until November (Figure 7b).

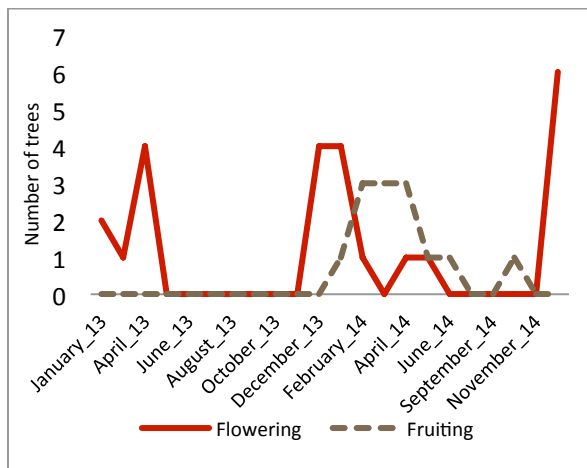


Figure 7a Flowering and fruiting of *Homalium guianense*

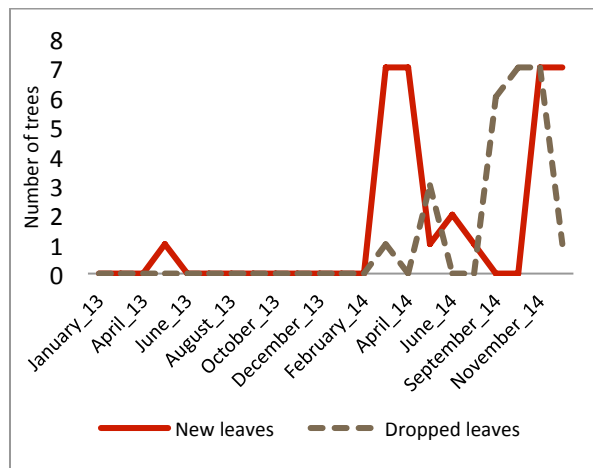


Figure 7b Leaf flushing and leaf fall of *Homalium guianense*

3.2 Canal transect

The phenophases from all trees on the canal transect were compared using a Friedman's Two Way analysis followed by Kendall's post-hoc analysis. No significance between the distribution of phenophases over the months was found ($P=0.388$). The different species from the Canal transect were also analyzed, for which all species with more than 7 individuals on the transect are used. These species included *Pterocarpus officinalis*, *Pentaclethra macroloba*, *Pachira aquatica*, *Prioria copaifera* and *Amanoa guianensis*. *Pterocarpus officinalis* showed a flowering peak in the end of November and a fruiting peak in the beginning of December (Figure 8a). The production of new leaves and the falling of leaves seemed to be relatively stable (Figure 8b).

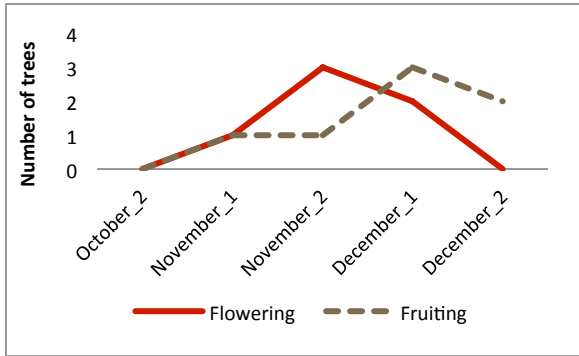


Figure 8a Flowering and fruiting of *Pterocarpus officinalis*

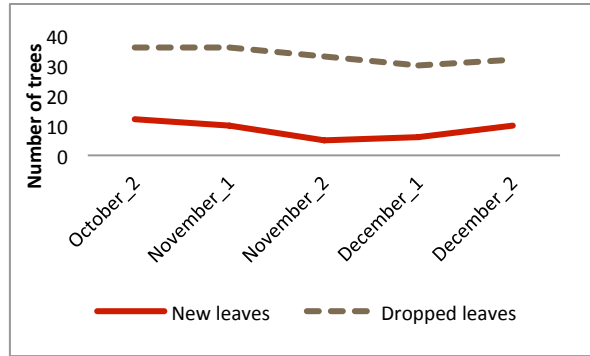


Figure 8b Leaf flushing and leaf fall of *Pterocarpus officinalis*

The amount of flowers of *Pentaclethra macroloba* decreased in the months the data was collected. The production of fruit was stable (Figure 9a). The production of new leaves had a small peak at the end of November and the dropping of leaves went from a small peak in the first part of November until the lowest point in the first part of December (Figure 9b).

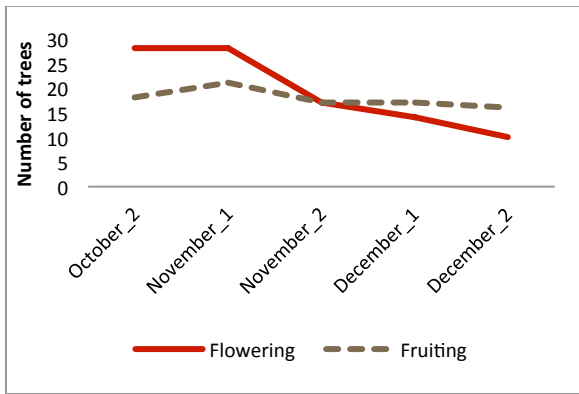


Figure 9a Flowering and fruiting of *Pentaclethra macroloba*

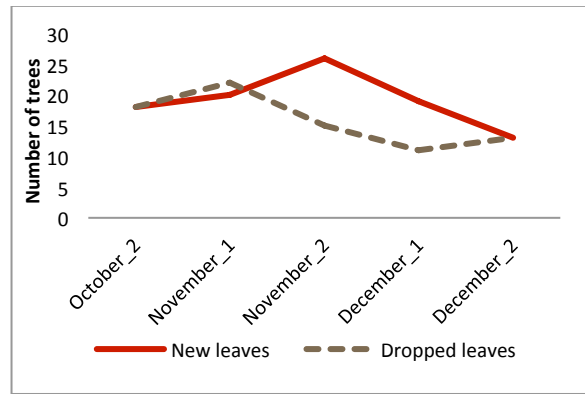


Figure 9b Leaf flushing and leaf fall of *Pentaclethra macroloba*

The *Pachira aquatica* showed a small peak in the flowering in the beginning of November and a small drop in the beginning of December. The fruiting kept stable over the period of time (Figure 10a). The leaf fall and leaf production both had a peak in the end of October and the beginning of November and dropped until the beginning of December (Figure 10b).



Figure 10a Leaf flushing and leaf fall of *Pachira aquatica*

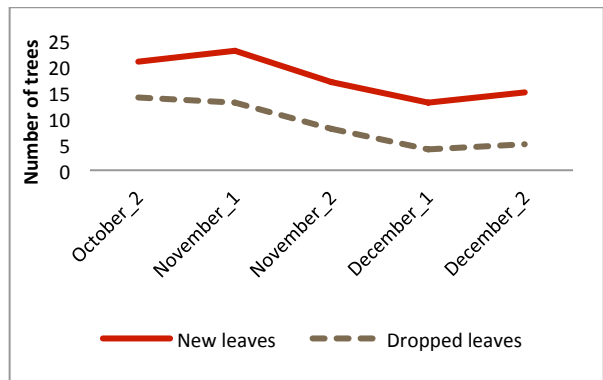


Figure 10b Flowering and fruiting of *Pachira aquatica*

The flowering of *Prioria copaifera* had a peak in October and dropped after that, the fruiting had a small peak in the end of November (Figure 11a). The production of new leaves only declined during this study and the leaf fall had a peak in the beginning of November and decreased after that (Figure 11b).

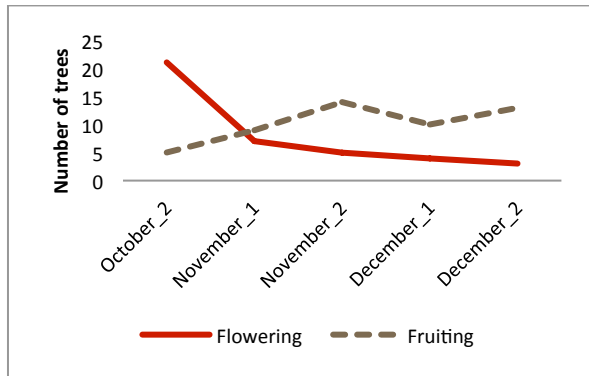


Figure 11a Flowering and fruiting of *Prioria copaifera*

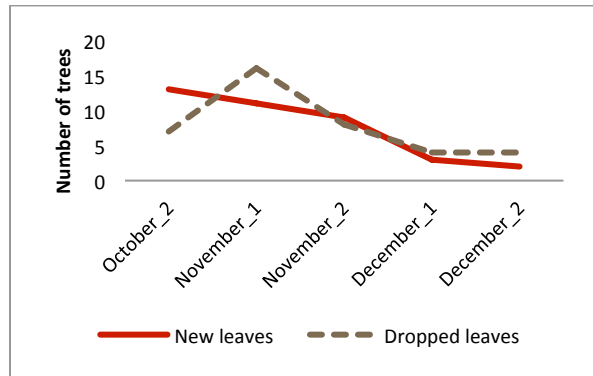


Figure 11b Leaf flushing and leaf fall of *Prioria copaifera*

Amanoa guianensis showed flowering and fruiting in all months (Figure 11a), a great amount of fruits was observed and almost all the trees had constant flowers on them of which a part was dead. The leaf flushing was relatively stable with a small drop in the end of November and after that a small peak in the beginning of December and the leaf fall only declined (Figure 11b).

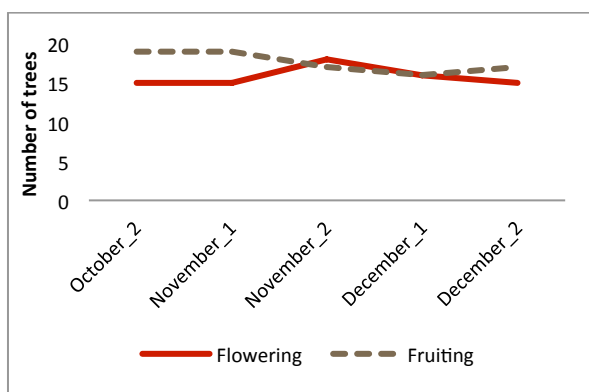


Figure 11a Flowering and fruiting of *Amanoa guianensis*

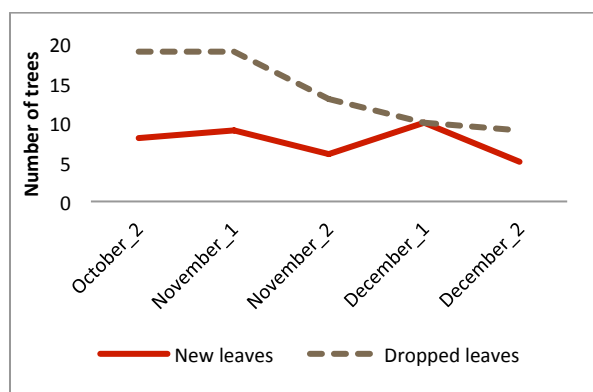


Figure 11b Leaf flushing and leaf fall of *Amanoa guianensis*

3.3 Comparison between the two transects

To examine differences between the two transects, the phenophases of all trees together were compared. The same pattern in flowering was seen between the canal and the jungle, both showing a slight decrease over the study period (October through December 2014). The amount of fruits was stable on both transects (Figure 12a). The production of new leaves was stable on the jungle transect, on the canal it had a slight drop from the beginning of November until the beginning of December. The amount of leaf fall of the jungle transect rose in October and stays stable after that, the leaf fall of the canal transect has a peak in the beginning of November and drops after that (Figure 12b).

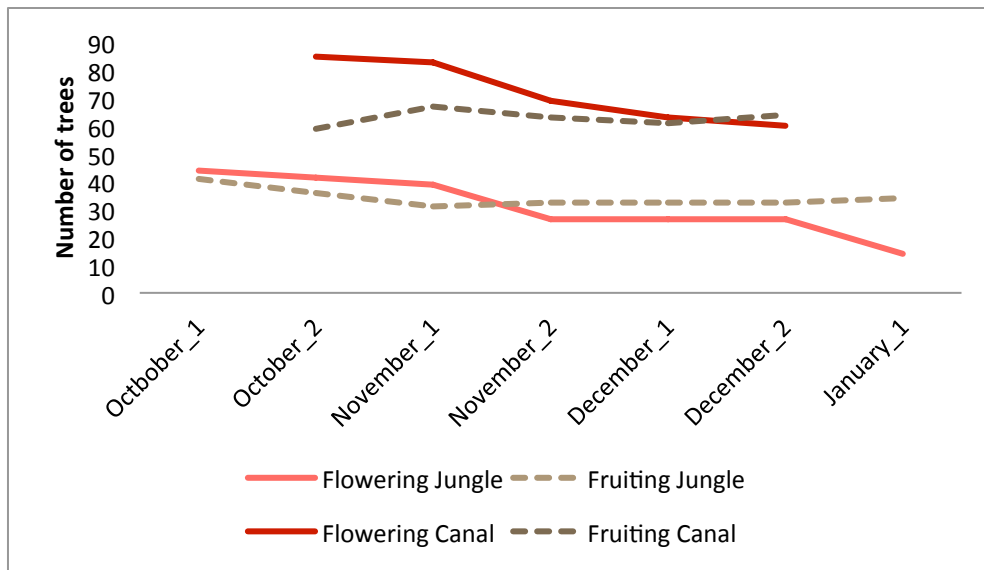


Figure 12a Flowering and fruiting of all trees in the transects

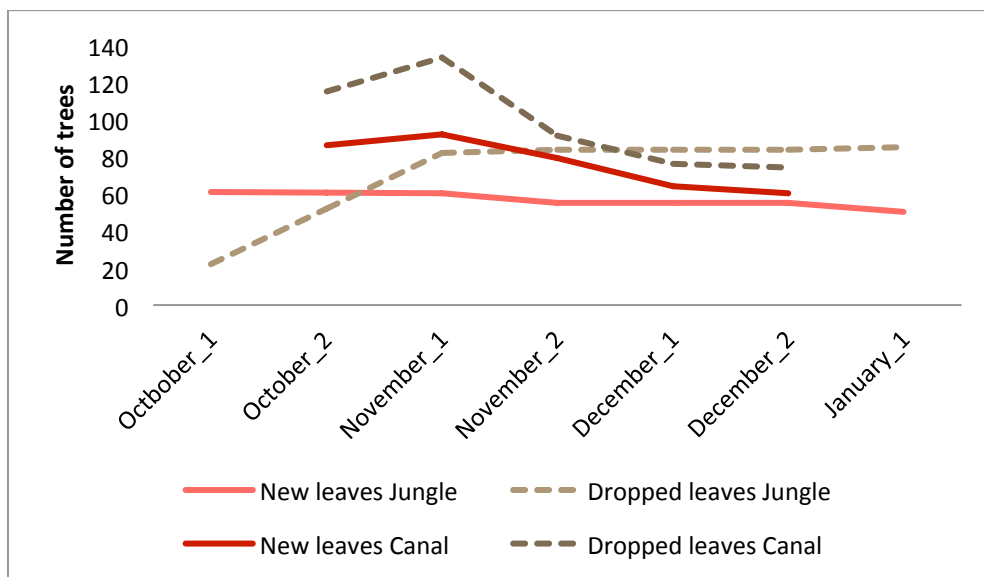


Figure 12b Leaf flushing and leaf fall of all trees in the transects

Because the composition of species of the transects differed, comparison of different species across the two transects is not possible for all species. Also not all species have enough individuals in the transects. For this reason only *Pentaclethra macroloba* was analyzed because there were enough individuals in both transects. In both transects a decrease in flowers was seen from October to January (Figure 13a). The amount of fruit stays stable over time (Figure 13b). The production of new leaves and the leaf fall did not show the same pattern between the two transects. The leaf flushing in the forest kept stable while the leaf flushing on the canal peaked at the end of November (Figure 13c). The leaf fall of the jungle transect rose from October until January while on the Canal transect it peaked in the beginning of November and dropped off in the beginning of December (Figure 13d).

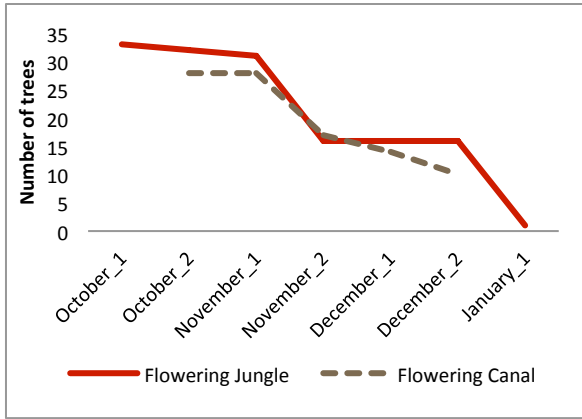


Figure 13a Flowering of *Pentaclethra maculoba* in the jungle and canal transects

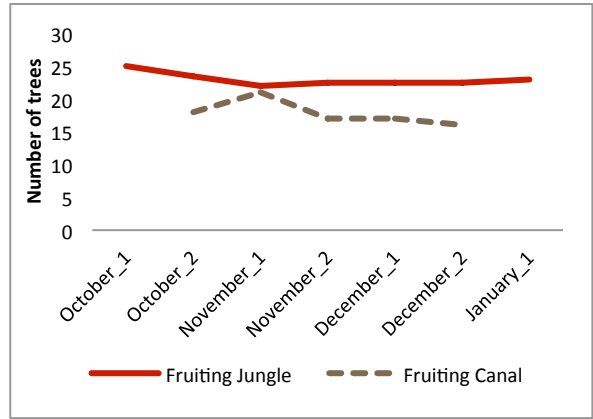


Figure 13b Fruiting of *Pentaclethra maculoba* in the jungle and canal transects

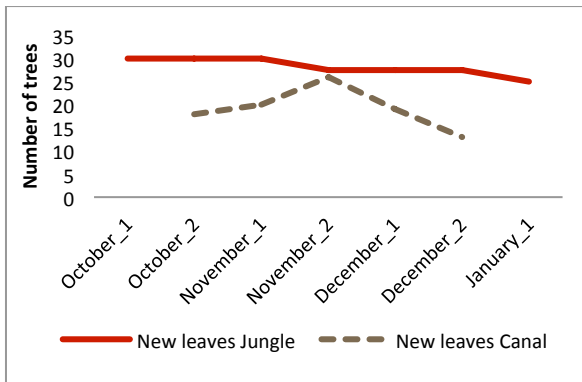


Figure 13c New leaves of *Pentaclethra maculoba* in the jungle and canal transects

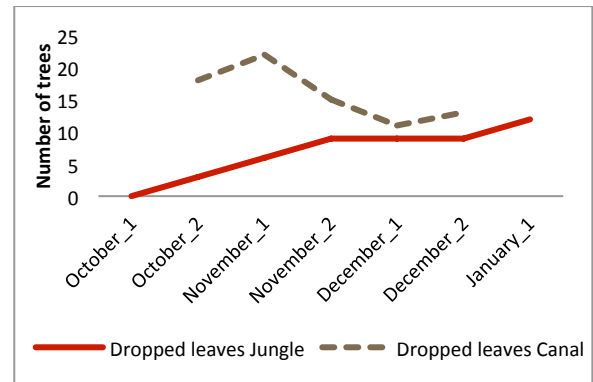


Figure 13d Leaf fall of *Pentaclethra maculoba* in the jungle and canal transects

4. Discussion

4.1 Jungle transect

On the jungle transect a flowering peak was seen from February until July, a fruiting peak from June until November and a leaf flushing peak from February until May. The weather in the study region is very unpredictable and it can change from year to year. It mostly is rainy with a slightly dryer season from late January until April and a second, less noticeable, dry season from August until October (Baker *et al.*, 2013). These seasons are recognizable in the phenology data of the jungle, with the flowering peak corresponding to the dry season and the fruiting peak logically following. The production of new leaves also coincides with the dry season. The leaf fall showed no distinct pattern, perhaps because this phenophase was only documented starting in 2014, so no long-term data was available.

Pentaclethra maculosa showed a flowering peak in May - July and October - December, which corresponds to other research that found flowering peaks from April until May and from August until December. Fruits seemed to be present the whole year, which can be explained by the fact that the tree retains the fruits for a long time (Orwa *et al.*, 2009). Most of the growth and leaf production is in the dry season (Flores, n.d.) as seen in the production of new leaves from September until April with a decrease from December until February. *Vochysia ferruginea* showed flowering from March until July which corresponds with research from Müller & Sánchez (n.d.), also done in the North of Costa Rica, who found flowering between March and June. The same study from Müller & Sánchez reported that fruiting varies among individual trees and over time. However, this phenology study showed a clear pattern of fruiting over the years, three months after the flowering peak. The production of new leaves started in the dry season and went on through the wet season, from March until July. *Apeiba membranacea* showed a flowering period twice a year. The fruiting period was from January until June which overlaps with a fruiting period found in previously research (Salazar & Soihet, 2001) from March until August. *Carapa nicaraguensis* showed a flowering and fruiting peak twice annual with fruits present almost the whole year. This fruiting pattern corresponds with a study by Kenfack (2011) that shows fruiting is possible the whole year. *Malouetia guatemalensis* had twice annual flowering peak, namely February until May and October until November which is in the dry seasons. Not much fruits were produced, only small peaks in April and July were seen, which is the wet season. Also according to T. B. Croat (n.d.) this tree flowers in the dry season and produces fruit in the wet season. *Homalium guianense* had twice annual flowering from December until January and from April until May, this fits right in the wet season.

4.2 Canal transect

Since the transect on the canal was only recently established, only three months of phenological data exist. This limited time period is not enough to draw conclusions, which is perhaps why no significant patterns were found during the study period. Some vague patterns were detected, but data from several years is necessary to draw any conclusions.

4.3 Comparison between the two transects

The environment of the two transects is rather different; the trees next to the canal receive more sun than the trees in the jungle which may affect phenology. Another factor influencing and exacerbating differences in the data collected could be the effect of the environment on the observer, as the trees in the forest are higher and closer together which can reduce the visibility. In flowering and fruiting

no difference was seen between the two transects. However there were marked differences in the production of new leaves and the leaf fall. The production of new leaves in the jungle stayed the same while the production of new leaves on the canal transect declined in November and December. The higher amount of fallen leaves in the jungle could be explained by the smaller amount of light available (Adams, 1976) or because the jungle was flooded from November until January what caused an oxygen lack for the trees (Burton, n.d.). The influence of a different environment is also shown by *Pentaclethra macroloba* which showed different leaf flushing and leaf fall between the two transects. Another study has shown that *Pentaclethra macroloba* is a shade-tolerant tree and that the production of leaves can decline if too much direct sun is present (Oberbauer *et al.*, 1986). This is also seen in this study where *Pentaclethra macroloba* trees in the jungle receive less light than the trees along the canal. This can also explain the high amount of leaf fall on the canal transect.

5. Conclusion

This study aimed to understand the influence of the weather and environment on the phenological pattern of trees in the jungle. Trees in general tend to show more flowering, fructification and leaf flushing in dryer periods. Leaf fall showed no distinct pattern which might be explained by the lack of data on this phenophase. Also this study has shown different phenological patterns per species. Some species tend to have a flowering peak in a dry season and other show flowering in a wet season. The influence of the environment where the tree grows in was seen for some species, likely due to different amounts of light and/or water. To know the precise cause further research needs to be done to see what resources the trees in both transects have available. Knowing when trees are producing flowers and fruits could be important so this could be monitored and the available food sources for animals are known. Also phenology is a way of understanding the ecosystem dynamics and discovering/documenting what potential effects climate change has on rainforests.

Ongoing research is required to better document and understand species-specific phenology and long-term trends and changes in rainforest tree phenology. In addition to continuing data collection in the future, it is important data are collected by the same observer or people trained by this observer so the data is not missing or biased.

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Appendix

Table 1 List of all trees in the jungle transect with scientific name, family and total count

Scientific name	Family	Total count	
Unknown	-	1	
<i>Xylopia sericophylla</i> Standl. & L.O. Williams	Annonaceae	1	
<i>Malouetia guatemalensis</i> (Müll. Arg.) Standl.	Apocynaceae	11	
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	Araliaceae	1	
<i>Hirtella</i> sp	Chrysobalanaceae	2	
<i>Clusia</i> sp	Clusiaceae	1	
<i>Alchornea costaricensis</i> Pax & K. Hoffm.	Euphorbiaceae	1	
<i>Alchorneopsis floribunda</i> (Benth.) Müll. Arg.	Euphorbiaceae	1	
<i>Crudia glaberrima</i> (Steud.) J.F. Macbr.	Fabaceae	1	
<i>Inga cocleensis</i> Pittier	Fabaceae	4	
<i>Inga</i> sp	Fabaceae	1	
<i>Pentaclethra macroloba</i> (Willd.) Kuntze	Fabaceae	47	
<i>Prioria copaifera</i> Griseb.	Fabaceae	4	
<i>Pterocarpus officinalis</i> Jacq.	Fabaceae	2	
<i>Zygia latifolia</i> (L.) Fawc. & Rendle	Fabaceae	2	
<i>Vismia macrophylla</i> Kunth	Hypericaceae	1	
<i>Vitex kuylenii</i> Standl.	Lamiaceae	3	
Lauraceae	Lauraceae	1	
<i>Byrsonima arthropoda</i> A. Juss.	Malpighiaceae	1	
<i>Apeiba membranacea</i> Spruce ex Benth.	Malvaceae	13	
<i>Pachira aquatica</i> Aubl.	Malvaceae	2	
<i>Sterculia recordiana</i> Standl.	Malvaceae	1	
<i>Theobroma simiarum</i> Donn. Sm.	Malvaceae	2	
Melastomataceae	Melastomataceae	2	
<i>Carapa nicaraguensis</i> C. DC.	Meliaceae	11	
<i>Ficus</i> sp	Moraceae	1	
Myrsinaceae	Myrsinaceae	1	
Myristicaceae	Myristicaceae	2	
<i>Virola koschnyi</i> Warb.	Myristicaceae	1	
<i>Heisteria concinna</i> Standl.	Olacaceae	1	
<i>Hyeronyma alchorneoides</i> Allemão	Phyllanthaceae	1	
<i>Cassipourea elliptica</i> (Sw.) Poir.	Rhizophoraceae	3	
Rubiaceae	Rubiaceae	2	
<i>Homalium guianense</i> (Aubl.) Oken	Salicaceae	7	
<i>Laetia procera</i> (Poepp.) Eichler	Salicaceae	2	
<i>Cupania</i> sp	Sapindaceae	1	
<i>Vochysia ferruginea</i> Mart.	Vochysiaceae	21	
	37	24	160

Table 2 List of all trees in the canal transect with scientific name, family and total count

Scientific name	Family	Total count	
Spondias mombin L.	Anacardiaceae	1	
Malouetia guatemalensis (Müll. Arg.) Standl.	Apocynaceae	1	
Maytenus guyanensis Klotzsch ex Reissek	Celastraceae	1	
Amanoa guianensis Aubl.	Euphorbiaceae	20	
Pterocarpus officinalis Jacq.	Fabaceae	42	
Pentaclethra macroloba (Willd.) Kuntze	Fabaceae	28	
Prioria copaifera Griseb.	Fabaceae	25	
Crudia glaberrima (Steud.) J.F. Macbr.	Fabaceae	7	
Zygia latifolia (L.) Fawc. & Rendle	Fabaceae	1	
Cynometra retusa Britt. Rose	Fabaceae- caesalpinoideae	1	
Zygia inaequalis Pittier	Fabaceae- mimosoideae	5	
Grias cauliflora L.	Lecythdaceae	3	
Pachira aquatica Aubl.	Malvaceae	25	
Luehea seemannii Planch. Triana	Malvaceae	1	
Carapa nicaraguensis C. DC.	Meliaceae	3	
Ficus maxima Mill.	Moraceae	1	
Ficus popenoei Stand.	Moraceae	1	
Ouratea curvata Engl. ex Dwyer	Ochnaceae	1	
Hyeronyma alchorneoides Allemão	Phyllanthaceae	1	
Homalium guianense (Aubl.) Oken	Salicaceae	7	
Coussapoa glaberrima Burger	Urticaceae	1	
	21	15	176