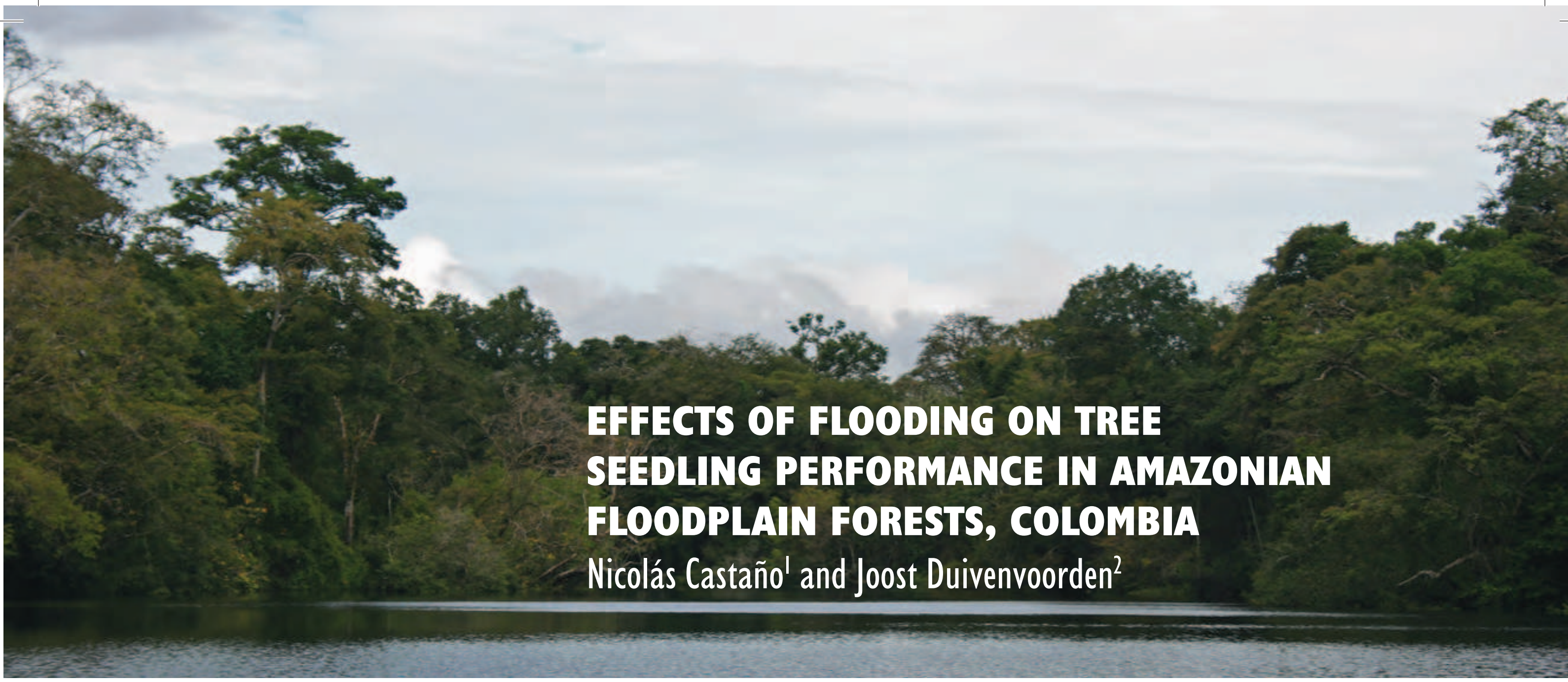

# EFFECTS OF FLOODING ON TREE SEEDLING PERFORMANCE IN AMAZONIAN FLOODPLAIN FORESTS, COLOMBIA

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## Abstract

A descriptive and experimental study of seedling growth of three timber species (*Pouteria* sp, *Eschweilera* sp, and *Mabea nitida*) as function of flooding was carried out in a low floodplain of the Mata-Mata River (Amacayacu National Park, Colombian Amazonia). Seedling growth of *Mabea nitida* was not affected by flooding. Seedlings of *Pouteria* and *Eschweilera* showed a reduced growth when completely submerged by floodwater. Seedlings of *Pouteria* and *M. nitida* with more leaves showed a faster growth. All seedlings were affected by herbivory. Spiders and fungi affected about one fourth to one third of all seedlings. Flooding reduced the attacks by spiders and fungi on seedlings from all species, and reduced herbivory on seedlings from *Pouteria*. Influence from soil nutrient availability or canopy openness on seedling growth was not detected.



## Keywords

Seedling Growth, Herbivory, Pathogen Attack, Canopy Openness, Amazon floodplain.



## Keywords

Seedling Growth, Herbivory, Pathogen Attack, Opening the Canopy, Amazonia, Flooded Forests.



## Resumen

Evaluamos el crecimiento de plántulas de tres especies maderables (*Pouteria* sp., *Eschweilera* sp., y *Mabea nitida*), en bosques inundables de la quebrada Matamata (Parque Nacional Natural Amacayacu, Amazonia colombiana), a través de un estudio descriptivo en campo y un experimento en función de la inundación.

El crecimiento de las plántulas de *Mabea nítida* no se afectó por la inundación. Las plántulas de *Pouteria* y *Eschweilera* presentaron una reducción en su crecimiento en los momentos en los que se encontraban sumergidos bajo el agua. Las plántulas de *Pouteria* y *M. nitida* presentaron más hojas y mostraron mayor crecimiento. Todas las plántulas fueron afectadas por herbovoría. Las arañas y los hongos afectaron entre un cuarto y un tercio de todas las plántulas. La inun-



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dación redujo el ataque de arañas y hongos sobre las plántulas de todas las especies y redujo la herbivoría sobre las plántulas de de *Pouteria.* No se detectó ninguna influencia de la disponibilidad de los nutrientes del suelo ni apertura del dosel sobre el crecimiento de las plántulas.

## Palabras clave

Crecimiento de plántulas, herbivoría, ataque de patógenos, apertura del dosel, Amazonia, bosques inundables.

## Introduction

Many factors determine the rates of tropical tree growth, such as light (Denslow 1980, Kobe 1999, Nicotra *et ál.,* 1999, Montgomery & Chazdon 2002), soil water availability, soil nutrient level (Baker *et ál.*, 2003), herbivory (Blundell & Peart 2001) and flooding (Parolin 2002). In floodplain forests, the soil surface is covered by water for several months and plants must survive in stress conditions due to, among others, lack of oxygen, reduced PAR (Photosynthetically Active Radiation), and high levels of potentially toxic compounds (e.g. ferrous cations). Roots of terrestrial plants and even entire plants that occur in the understory of floodplain forests are subjected to a yearly submersion for about 50-270 days (Junk 1989). Especially in low floodplain areas where flooding takes place most frequently and during long spells, these stress conditions are relevant for seedling growth. On the other hand, flooding might also give seedlings the advantages of reduced seedling herbivory or pathogen attack and a potentially extra soil nutrient input (the latter especially in várzea systems). The relationship between plant damages by herbivory or pathogens and flooding can be seen in two ways: 1) a change in hydroperiod might introduce physiological stress in a floodplain plant (Osmond *et ál.*, 1987), which in turn reduces its resistance or tolerance to damage (Mattson & Haack 1987) and 2) a change in hydroperiod can modify foraging behaviour or population density of pathogens and herbivores (Hoslett 1961, Sheppe & Haas 1981, Andersen & Cooper 2000). Pathogens and herbivory are expected to have a more negative impact on growth and survival of plants when other environmental variables limit the plant's ability to compensate for losses caused by herbivores and pathogens (the plant stress hypothesis; Crawley 1997). In agreement with these predictions, flooded plants often experience higher mortality from more frequent attacks by herbivores and pathogens than plants not subjected to inundation (Davison & Tay 1987, Mori & Becker 1991).

If and how seedlings grow and die in Amazonian floodplains as a possible consequence of flooding, herbivory, and pathogen attack is poorly documented (Parolin 2002, Parolin *et ál.*, 2004). Apart from this, much information about the regeneration of tree species along the gradients of flooding or other environmental site conditions in Amazonian floodplain forests is still lacking (Wittmann & Junk 2003).

The general objective of this study was to quantify seedling growth of three timber species in a low floodplain of an Amazonian river in southern Colombia, in response to flooding and other environmental and biological variables. We studied *in situ* growth of seedlings as function of flooding, herbivory, two environmental conditions (light, soil), and seedling properties. Parallel to this we carried out a manipulative experiment to compare the effects of simulated flooding on transplanted seedlings.

## Methods

### Study site

We conducted this study in the Amacayacu National Park (between 3° 49´ - 3° 02' S and 69° 54' - 70°15´W), Amazon department, Colombia. The mean monthly temperature here ranges from 25.1° (June) to 26.4° (October). Annual rainfall averages 2836 mm and monthly rainfall 268 mm. The rainfall regime is unimodal (Castaño-Uribe & Cano 1998). The season with less rain is in June-September and with most rain in January-April. The studied forest formed part of the floodplain of the Mata-Mata River. In a straight line the study area was between 1.5 and 3.2 km away from the mouth of this river into the Amazon River. The floodplain is filled up by fluvial sediments derived from Tertiary sediments (Pebas Formation; Hoorn 1991, Arbelaez *et ál.*, 2008). Because of the proximity to the Amazon River the occasional inflow of water from this river and the deposition of its sediments likely occur. The water level of the Mata-Mata River is mostly determined by the fluctuations of the Amazon River. The low water level season is generally between July and February.

The floodplain area is located close to Mocagua Indigenous Reserve. The forest here is relatively undisturbed and in use for occasional extraction of wood and non-wood products, including hunting and fishing, but not for clear-cutting. Recently, 77 tree species were found among 177 individuals (>2.5 cm DBH) in a small plot of 0.1 ha in these forests (Restrepo 2002). The floodplain forest has an average canopy height of 24 m and contains trees with a thicker maximum diameter than found in nearby terra firme and swamp forests (Restrepo 2002). The most frequently found species in this floodplain forest are *Maquira coriacea* (Moraceae), *Campsiandra angustifolia* (Caesalpiniaceae), *Coccoloba williamsii* (Polygonaceae) and *Ficus insipida* (Moraceae) (Restrepo 2002). The fieldwork was done between November 2004 and February 2005, which was a period characterized by small water level fluctuations, just prior to the big annual rise of water level of the Amazon River.

## Studied species

Three tree species, which had seedlings growing in the low floodplain area of the Mata-Mata River, were selected for this study. These species were chosen as they occurred with a high number of seedlings at various levels of the low floodplain. The selected species were: 1) *Mabea nitida* Spruce ex Benth. (Euphorbiaceae), called "siringarana". According to local informants the seeds from this species are eaten by fish; 2) *Eschweilera* sp. (Lecythidaceae), called "golondrino". This is a timber tree and its young stems are used as fishing rod by local people; and 3) *Pouteria* sp. (Sapotaceae), called "caimitillo", and also a timber tree. These three species did not show special adaptations to flooding such as adventitious roots or stem hypertrophy. Two kinds of leaf damage were recorded: fungi that generate dead tissue and spiders that bend the leaves to build their 'house'. Both these damages were called pathogen attack, because they reduced the photosynthetic leaf area considerably. Herbivory, by which substantial parts of leaves were consumed or removed, was mostly seen done by caterpillars and ants.

## Data collection

In the low floodplain of the Mata-Mata River, seedlings of the three studied species were selected as close as possible to sampling points. These points were located using a random table (one digit for the distance between sampling points, the second for the number of seedlings selected at a sampling point, and the third for the direction to establish a new sampling point). Only seedlings lower than 90 cm height were included. Seedlings were measured *in situ* and *ex situ* (experimental transplantation).

### • *In situ* measurements

A total of 791 seedlings (259 *M. nitida*, 246 *Eschweilera*, 286 *Pouteria*) were marked, mapped, and measured in three measurement periods (15 Nov. to 30 Nov. 2004; 13 Dec. to 17 Dec. 2004; and 4 Jan. to 11 Jan. 2005). For each seedling we recorded uppermost bud height, number of leaves, number of leaves with herbivory attack, herbivory percentage (the average of the visually estimated proportion of leaf areas affected by herbivory), leaf damage by spiders or fungi, and canopy openness directly above each seedling (recorded by means of a Spherical Densiometer type Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, USA, Model –A). In addition, the floodplain level at which each seedling occurred, was recorded relative to the water level of the river using vertical poles. For each seedling the number of days of inundation (river water reaching but not yet fully submerging the seedling) and complete submersion was inferred from the elevation of its growing position in the floodplain and the water level fluctuations. These latter were recorded daily and calibrated back to the scales of the Meteorological Station of Amacayacu Park (located at the mouth of the Mata-Mata River into the Amazon River).

### • *Ex situ* measurements (manipulative experimental set-up)

A total of 306 seedlings of the studied species (117 *M. nitida*, 90 *Eschweilera*, 99 *Pouteria*) were randomly selected. These seedlings were carefully removed from the forest soil with a considerable amount of soil around their roots (approximately 30 $cm^3$) in order to avoid root damage. Subsequently the seedlings were randomly mixed and planted into 14 specially prepared wooden boxes of 1.8 m x 30 cm x 50 cm depth. These boxes were previously filled with a thoroughly mixed sample of mineral soil taken from ten different locations in the low flood plain of the Mata-Mata River. In the boxes the seedlings were planted about 20-40 cm apart from each other. Supported by ropes six randomly picked boxes (all together containing 76 *M. nitida*, 36 *Eschweilera*, 50 *Pouteria* seedlings) were submerged in such a way that all seedlings were completely below the water level during a total continuous period of 55 days, from 25 November to 20 January. According to the fluctuations of the river water level these boxes were lifted up and down each day in order to keep seedling tops at approximately 30 cm or less below the water surface. The other boxes (which contained 41 *M. nitida*, 54 *Eschweilera*, 49 *Pouteria* seedlings) were put on a floating raft construction (Figure 1), which was covered by shading cloth, in order to homogenize the conditions of incoming radiation on to the seedlings. The transplanted seedlings were measured in a similar fashion as to the *in situ* seedlings (except for canopy openness, seedling diameter and presence of spiders and fungi), in two measurement periods (17-18 December 2004 and 17-18 January 2005).

## Soil sampling and laboratory analysis

In the area where the seedlings were sampled, five points were randomly selected at least 20 m apart from each other. At each point, a soil sample was taken at 0-5 cm depth (after removal of superficial organic horizons) at 0 cm, 30 cm, 60 cm and 90 cm above the water level (corresponding to 10.90, 11.20, 11.50 and 11.80 m along the scales of the Meteorological Station of Amacayacu Park, respectively). Each soil sample was stored in a plastic bag, and dried to air within 90 days after the sampling.

Soil analyses were conducted at the Soil Laboratory of the Instituto 'Agustín Codazzi' in Bogotá. These concerned (full methods in IGAC, 1990): pH ($H_2O$) in a volumetric 1:1 soil: water solution; C according to the Walkley-Black method; available P by extraction with

**FIGURE 1**. EXPERIMENTAL BOXES. FLOATING STRUCTURES WERE MADE WITH FLOATING WOOD, COLLECTED FROM AMAZON RIVER. NOTE THAT THE SHADING CLOTH IS NOT VISIBLE.

0.1N HCl and 0.13 N NH4F, according to BrayII; exchangeable bases after extraction with NH4OAc 1N (pH=7) with Ca and Mg complexed with EDTA, and Na and K measured by flame photometry; exchangeable acidity by extraction in 1N KCl and titration with 0.1 N NaOH in the presence of phenolphtalein; cation exchange capacity (CEC) with the 1 N NH4OAc (pH=7) method.

### *Data Analysis*

The soil chemical variables were tested for differences between elevation by means of ANOVA, followed by Tukey–Kramer HSD post-hoc comparison tests (with a significance level of 0.05), in case of significant differences. Subsequently, soil samples were classified in two fertility groups, as follows:

if elevation < 11.10 m then soil fertility factor = 1, otherwise soil fertility factor = 0

For each seedling that survived during the measurement period, the growth rate in height (GR) was calculated as:

$$GR = (H_2 - H_1) / (t_2 - t_1)$$

where: $H_1$ = height at $t_1$; $H_2$ = height at $t_2$; $t_1$ = time of the first height measurement and $t_2$ = time of the last measurement.

For each species separately, GR was tested against a suit of explanatory variables in multiple regression, using forward selection (in JMP 3.0 for the Macintosh; applying default settings). The explanatory variables were initial height, number of leaves, days of inundation, days of submersion, canopy openness, percentage of herbivory, presence of spiders, presence of fungi and the soil fertility factor (poor = 0, fertile = 1; see further). The spider, fungi and soil factor variables were entered as binary variables. In the regression analysis of the flooding experiment, the flooding treatment was entered as a binary variable (with flooding = 1, no flooding = 0), but days of inundation, days of submersion, canopy openness, and the soil fertility factor were excluded, as these were constant. Also the presence of spiders and fungi were excluded as these were assumed to die or migrate during the inundation (Adis 1997). Before regression and ANOVA, skewness of not-normal variables was reduced by transformations (square root of GR, and natural logarithm of herbivory, days of inundation, days of submersion, canopy openness, initial height, number of leaves, and the soil chemical variables apart from pH). Differences in herbivory and GR due to flooding treatments were tested by Mann-Whitney tests. Spearman rank correlation coefficients were calculated between flooding variables, herbivory percentage, and pathogen attack, derived from the *in situ* measurements. All these analyses were made in r version 2.10.

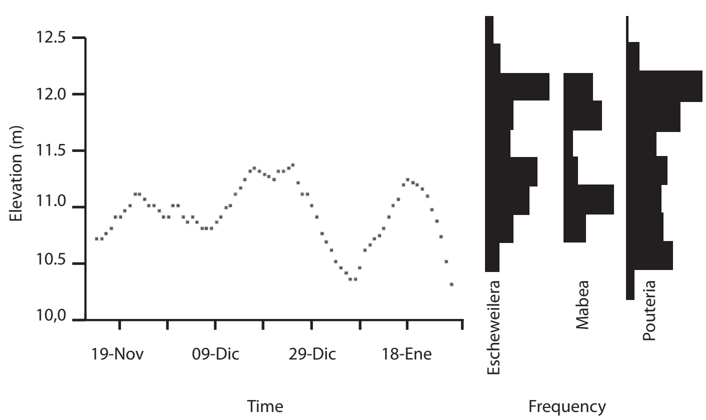


**FIGURE 2** WATER LEVEL OF THE MATA-MATA RIVER IN THE STUDY PERIOD, ACCORDING TO THE SCALING USED AT THE METEOROLOGICAL STATION OF AMACAYACU PARK, AND SAMPLING ELEVATION OF THE *IN SITU* SEEDLINGS, PRESENTED IN CLASSES (BAR WIDTH) OF 0.5 M.

**TABLE 1.** SOIL CHEMICAL ANALYSES OF FIVE SAMPLES, EACH TAKEN AT 0-5 CM DEPTH OF THE MINERAL SOIL AT FOUR DIFFERENT ELEVATIONS IN THE FLOODPLAIN OF THE MATA-MATA RIVER. IN CASE OF SIGNIFICANT DIFFERENCES BETWEEN DEPTHS, THE SMALL LETTERS DENOTE THE RESULTS OF TUKEY–KRAMER HSD POST-HOC COMPARISON TESTS (WITH A SIGNIFICANCE LEVEL OF 0.05)* 0.01 <= P < 0.05; ** 0.001 <= P < 0.01; *** P < 0.001.

| Elevation (m) | pH | Ca | Mg | K | Na | CEC | Acidity | C | P |
|---|---|---|---|---|---|---|---|---|---|
| | cmol(+)/kg | | | | | | | % | mg/kg |
| | mean ± one SD | | | | | | | | |
| 10.90 | 3.6 ± 0.2 | 1.6 ± 1.5 | 0.8 ± 0.2a | 0.5 ± 0.1 | 0.2 ± 0.1a | 44.8 ± 3.7 | 12.6 ± 2.3 | 7.3 ± 1.3 | 12.0 ± 6.8 |
| 11.20 | 3.6 ± 0.2 | 0.7 ± 0.4 | 0.5 ± 0.1b | 0.4 ± 0.1 | 0.1 ± 0.0ab | 46.5 ± 2.0 | 12.7 ± 2.3 | 6.9 ± 1.8 | 13.3 ± 5.4 |
| 11.50 | 3.6 ± 0.3 | 0.8 ± 0.7 | 0.6 ± 0.2ab | 0.4 ± 0.0 | 0.1 ± 0.1ab | 46.1 ± 7.4 | 13.9 ± 1.8 | 6.8 ± 1.1 | 8.2 ± 1.1 |
| 11.80 | 3.5 ± 0.1 | 0.7 ± 0.6 | 0.5 ± 0.1ab | 0.5 ± 0.1 | 0.1 ± 0.0b | 48.6 ± 5.7 | 9.5 ± 7.9 | 6.4 ± 1.7 | 12.0 ± 5.5 |
| F | 0.4 | 1.1 | 3.9* | 0.9 | 4.0* | 0.4 | 1.8 | 0.4 | 0.8 |

## Results

### *In situ measurements*

During the period of field measurements the water level of the Mata-Mata River varied between 10.0 and 11.5 m according to the scaling at the meteorological station at the mouth of the river, and three peaks were visible (Fig. 2). The soil analyses showed that at the lowest elevation soils were relative rich in cations (Table 1). For this reason samples take at elevations below 11.10 m were classified as 'fertile', and those taken above this level as 'poor'. Seedlings were sampled at elevations between 10.00 and 12.50 m (Fig. 2). Due to the water level fluctuations of the Mata-Mata River, the seedlings were inundated during a total period of 0 to 75 days, and submerged during a total of 0 to 71 days. The majority of seedlings suffered from a relatively short period of flooding (Fig. 3)

On average, *M. nitida* seedlings were most thin and small, and had the lowest number of initial leaves (Table 2). *Eschweilera* seedlings had a higher number of leaves but they were as tall as *M. nitida. Pouteria* seedlings were considerably taller (Table 2). The canopy openness above the *in situ* seedlings varied between 2.9% and 38.7%, and was about 10% on average (Table 2). For each species the canopy openness was not correlated with height (Spearman r < 0.1, p > 0.30. For *Pouteria* and *M. nitida*, canopy openness was also not related to the number of

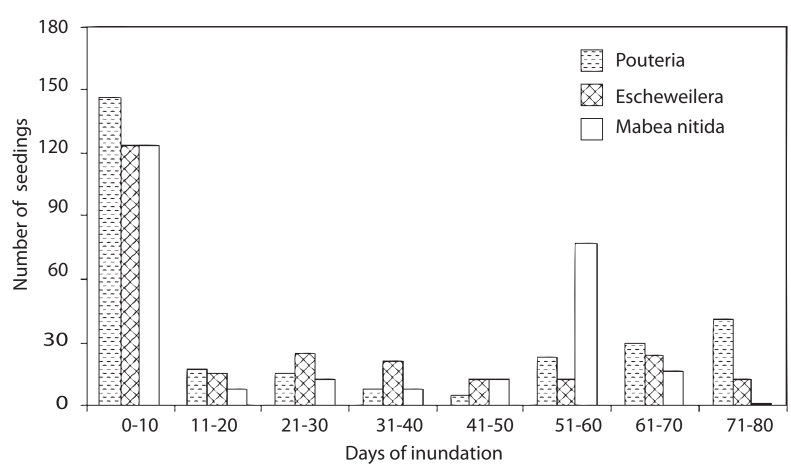


**FIGURE 3.** NUMBERS OF *IN SITU* SEEDLINGS PER 10-DAY INUNDATION INTERVAL

**TABLE 2.** INITIAL PROPERTIES, CANOPY OPENNESS, AND GROWTH RATE (GR) OF *IN SITU* SEEDLINGS.

| | Diameter (cm) at height of | | Number of leaves | Height (cm) | Canopy openness (%) | Growth rate (cm/day) |
|---|---|---|---|---|---|---|
| | 0 cm | 2 cm | | | | |
| | mean ± one SD | | | | | |
| Pouteria | 3.9±1.2 | 3.6±1.3 | 8.8±4.4 | 33.9±12.9 | 10.6 ± 2.9 | 0.034 ± 0.038 |
| Eschweilera | 2.7±0.6 | 2.3±0.5 | 9.7±4.1 | 18.7±5.1 | 10.5 ± 3.5 | 0.021 ± 0.027 |
| M. nitida | 2.4±0.8 | 2.2±0.5 | 3.4±4.2 | 19.6±8.6 | 9.7 ± 3.1 | 0.015 ± 0.025 |

**TABLE 3.** NUMBER OF SEEDLINGS WITH HERBIVORY AND PATHOGEN ATTACKS, AND PROPORTION OF HERBIVORY DAMAGE PER SEEDLING, FOR *IN SITU* SEEDLINGS OF *POUTERIA*, *ESCHWEILERA*, AND *MABEA NITIDA*.

| | Number of seedlings | | | | Herbivory damage (%) |
|---|---|---|---|---|---|
| | Total | With herbivory | With spiders | With fungi | |
| Pouteria | 276 (100%) | 276 (100%) | 33 (12%) | 15 (5%) | 13.2 ± 12.9 |
| Eschweilera | 240 (100%) | 240 (100%) | 28 (11%) | 8 (3%) | 8.4 ± 9.3 |
| M. nitida | 253 (100%) | 227 (90%) | 34 (13%) | 25 (10%) | 10.5 ± 14.0 |

**TABLE 4.** SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN VARIABLES OF FLOODING (DAYS OF INUNDATION AND DAYS OF COMPLETE SUBMERSION), HERBIVORY, AND PATHOGEN ATTACKS, RECORDED ON THE *IN SITU* SEEDLINGS OF *POUTERIA*, *ESCHWEILERA*, AND *MABEA NITIDA*. * 0.01 <= P < 0.05; ** 0.001 <= P < 0.01; *** P < 0.001.

| | Herbivory | Presence of spiders | Presence of fungi |
|---|---|---|---|
| Pouteria | | | |
| Days of inundation | -0.19** | -0.30*** | -0.16** |
| Days of submersion | -0.13* | -0.27*** | -0.15* |
| Eschweilera | | | |
| Days of inundation | -0.01 | -0.34*** | -0.12 |
| Days of submersion | -0.02 | -0.31*** | -0.11 |
| M. nitida | | | |
| Days of inundation | -0.07 | -0.37*** | -0.24*** |
| Days of submersion | -0.10 | -0.34*** | -0.27*** |

leaves or leaf density (number of leaves / seedling height) (Spearman $r < 0.04$, $p > 0.50$). The seedlings of *Eschweilera*, however, had more leaves (Spearman $r = 0.15$, $p = 0.016$) and a higher leaf density (Spearman $r = 0.14$, $p = 0.023$) under more open canopies. The canopy openness was negatively correlated with the elevation of the spots where each seedling was recorded (Spearman $r = -0.32$, $p < 0.001$ for *Pouteria*, $r = -0.34$, $p < 0.001$, for *Eschweilera*, and $r = -0.07$, $p = 0.24$ for *M. nitida*). This suggested that more PAR might be available for seedlings if they occurred closer to the water line.

Virtually all *in situ* seedlings were affected by herbivory (Table 3). On average, about 8 to 13% of the leaf area of individual seedlings was damaged by herbivory. Between 28% and 34% of the seedlings were affected

**TABLE 5**. RESULTS OF LINEAR MULTIPLE REGRESSION OF GR AGAINST VARIABLES OF FLOODING (DAYS OF INUNDATION, DAYS OF SUBMERSION), CANOPY OPENNESS, HERBIVORY PERCENTAGE, PATHOGEN ATTACK (PRESENCE OF SPIDERS OR FUNGI), THE SOIL FERTILITY FACTOR, AND PLANT PROPERTIES (INITIAL HEIGHT AND NUMBER OF LEAVES) OF SEEDLINGS OF POUTERIA, ESCHWEILERA, AND MABEA NITIDA. ONLY THE MODEL RESULTS AFTER FORWARD STEPWISE REGRESSION CONTROL ARE SHOWN. * 0.01 <= P < 0.05; ** 0.001 <= P < 0.01; *** P < 0.001.

| | adjusted R2 | F | Days of inundation | Days of submersion | Herbivory percentage | Soil factor | Initial height | Number of leaves |
|---|---|---|---|---|---|---|---|---|
| | | | partial standandized regression coefficients | | | | | |
| Pouteria | 0.05 | 5.8*** | | -0.19** | | | -0.10 | 0.20** |
| Eschweilera | 0.14 | 39.6*** | | -0.38*** | | | | |
| M. nitida | 0.06 | 5.2*** | -0.33 | | -0.08 | 0.24 | | 0.21** |

**TABLE 6.** INITIAL PROPERTIES (HEIGHT, NUMBER OF LEAVES), PROPORTION OF HERBIVORY DAMAGE PER SEEDLING, AND GROWTH RATE (GR) OF *EX SITU* SEEDLINGS.

| | Height (cm) | Number of leaves | Herbivory damage (%) | Growth rate (cm/day) |
|---|---|---|---|---|
| | Mean ± one SD | | | |
| Flooded seedlings | | | | |
| Pouteria | 27.2 ± 7.2 | 6.3 ± 2.8 | 12.3 ± 10.3 | 0.002 ± 0.008 |
| Eschweilera | 16.0 ± 3.9 | 5.1 ± 2.2 | 5.4 ± 4.4 | 0.004 ± 0.011 |
| M. nitida | 15.7 ± 5.5 | 2.9 ± 1.0 | 3.1 ± 4.4 | 0.005 ± 0.016 |
| Non flooded seedlings | | | | |
| Pouteria | 29.5 ± 10.1 | 6.4 ± 2.9 | 13.6 ± 10.6 | 0.016 ± 0.022 |
| Eschweilera | 14.6 ± 3.8 | 6.4 ± 3.1 | 9.1 ± 7.5 | 0.007 ± 0.015 |
| M. nitida | 25.0 ± 7.0 | 3.9 ± 1.8 | 10.5 ± 10.3 | 0.009 ± 0.021 |

**TABLE 7.** RESULTS OF LINEAR MULTIPLE REGRESSION OF GR AGAINST FLOODING TREATMENT), HERBIVORY PERCENTAGE, INITIAL HEIGHT, AND NUMBER OF LEAVES OF SEEDLINGS OF *POUTERIA*, *ESCHWEILERA*, AND MABEA NITIDA. ONLY THE MODEL RESULTS AFTER FORWARD STEPWISE REGRESSION CONTROL ARE SHOWN. * 0.01 <= P < 0.05; ** 0.001 <= P < 0.01; *** P < 0.001.

| | adjusted R2 | F | Flooding treatment | Herbivory percentage | Initial height | Number of leaves |
|---|---|---|---|---|---|---|
| | | | partial standandized regression coefficients | | | |
| Pouteria | 0.19 | 23.3*** | -0.45*** | | | |
| Eschweilera | 0.07 | 4.3* | | | -0.30** | 0.13 |
| M. nítida | 0.04 | 5.6* | | | 0.22* | |

by spiders, whereas fungi affected 8-25% of the seedlings (Table 3). Herbivory and pathogen attack to the *in situ* seedlings was negatively correlated to flooding (Table 4). The *in situ* seedling mortality was fairly low at the final measurement: *Pouteria* seedlings suffered the highest mortality percentage (3.5%), followed by *Eschweilera* seedlings (2.4%) and *M. nitida* seedlings (2.3%). The dead seedlings did not have presence of pathogens (neither spiders nor fungi).

The average GR of the species varied between 0.015 and 0.034 cm/day (Table 2). In the final model of the multiple regression, the number of leaves positively related to the GR of *Pouteria* and *M. nitida* seedlings (Table 5). Flooding in terms of days of submersion negatively influenced the seedling growth of *Pouteria* and *Eschweilera* (Table 5).

### *Ex situ flooding experiment*

ll *ex situ* seedlings for the flooding experiment were sampled at elevations between 11.30 to 11.80 m. This implied that all soil material, which adhered to the roots, belonged to the poor soil class. The growth rate of the transplanted seedling was two to four times lower than that of the *in situ* seedlings (Table 2 and 6). At the final measurement 4.0% of the *Pouteria* seedlings had died in the flooded boxes, and 6.1% in the unflooded boxes. For *Eschweilera* seedlings these mortality rates were 11.1% and 0.0%, and for *M. nitida* 7.9% and 7.3%, respectively.

The herbivory damage decreased significantly due to flooding treatment for seedlings of *Eschweilera* (Mann-Whitney test, $W = 1174$, $p < 0.001$) and *M. nitida* (Mann-Whitney test, $W = 2280$, $p < 0.001$). For *Pouteria* seedlings the herbivory damage (Table 6) did not differ between the flooded and the control treatment (Mann-Whitney test, $W = 1308$, $p = 0.34$).

The seedlings of *Pouteria* responded negatively in their growth rate to the flooding treatment (Table 6; Mann-Whitney test, $W = 1557$, $p < 0.001$). However, for the two other species flooding did not reduce their growth rate (*Eschweilera*: Mann-Whitney test, $W = 956$, $p = 0.23$; *M. nitida*: Mann-Whitney test, $W = 1490$, $p = 0.08$). A substantial number of seedlings (90% for *Pouteria*, 78% for *Eschweilera*, and 84% for *M. nitida*) did not show any growth in the flooded boxes. Also in the non-flooded boxes many seedlings did not show growth (49% for *Pouteria*, 76% for *Eschweilera*, and 73% for *M. nitida*).

Multiple regression of the GR against flooding, plant properties, and herbivory (Table 7) only yielded significant flooding effects for *Pouteria,* whereas the initial height turned out important for the other two species.

## Discussion

### *Flooding effects*

*In situ* seedling growth of *Eschweilera* and *Pouteria* was negatively affected by the duration of complete submersion. These results suggest that these species are poorly adapted to the floodplain ecosystem. Despite the delicate state of the seedlings of *M. nitida* (lowest number of initial leaves, smallest and thinnest seedlings) their growth rate was not influenced by flooding, suggesting a good adaptation to floodplains of this species. This corresponds to the suggestion by local informants that fish eats the seeds of this species. The rising water level reduced pathogen attacks (spiders and fungi) on the *in situ* seedlings. Flooding might affect the populations and foraging behaviour of spiders and regulate seedling attacks by fungi. The latter observations (fungi infection in relations to changing water levels), however, need confirmation by more field data. The way flooding reduced herbivory for *in situ Pouteria* seedlings suggests that the herbivores that attack this species are poorly adapted to flooding. Because the impact of both pathogens and herbivory on seedling growth was reduced in situations of flooding, support to the idea that flooding would increase the negative impact of pathogens or herbivory on the growth of seedlings was not obtained.

The seedling transplantation applied in the flooding experiments had negative effects on the seedling growth. Also, the comparatively high mortality of the *ex situ* seedlings evidenced the seedling sensibility to manipulative transportation. The flooding experiment confirmed the decrease in growth rate of *Pouteria* seedlings due to flooding, but was probably too short to show a flooding effect on the other two species. Worbes (1997) reported on a flooding-related reduction in growth rates of several floodplain tree species.

Overall, the seedling growth rates in this study were low. This is commonly found for seedlings in the understorey of rain forests (Swaine 1996). According to that review study the number of leaves generally have a high influence on seedling growth. Dickson & Isebrands (1991) proposed that leaves are major regulators of shoot development and carbon allocation within the whole plant. Other studies have found similar results for adult tropical plants (Pacheco 2001) and seedlings (Zagt 1997, Garcia-Guzmán & Benítez-Malvido 2003).

Also, the seedling mortality percentage was low, for all three species. This might be a consequence of the short duration of the study. The causes of seedling mortality were not clear. Dead seedlings presented no pathogen attack and their average herbivory percentages were close to that of the surviving seedlings. Neither canopy openness nor flooding had a relation with the mortality of the three species studied. Mammal foraging might be a strong cause of seedling dead, as has been reported for other tropical tree seedlings (Sork 1987).

### *Herbivory and PAR effects*

Herbivory was found on the three seedling species but its effects on seedling growth or mortality was not clear. Extreme herbivory has been reported as having significant effects on plant growth (Blundell & Peart 2001). Zagt (1997) also reported non-effects of two mortality factors (attack by fungi and herbivores) on height growth rates in the tree canopy seedlings. The same result has been found for Amazon tree palms, where herbivores did not determine differential mortality or growth of study species (Pacheco 2001).

Although microsite variation in direct and diffuse PAR availability has been reported as influential to plant growth in closed canopy understories (Chazdon 1986, Montgomery & Chazdon 2002), in this study PAR variation had no effect on seedling growth.

Floodplains often show lower plant densities than terra firme forests (Restrepo 2002, Cárdenas *et ál.*, 1997), possibly leading to higher PAR availability in the former. Evidence of strong growth responses to increases in PAR availability (Montgomery & Chazdon 2002) is generally obtained in upland forests, where PAR environments might be lower that in floodplain forests. The PAR distribution within the floodplain of the Mata-Mata River agrees with records from Wittman & Junk (2003) in the western Brazilian Amazon, where they found a small PAR gradient from the high to the low varzea forest. PAR might represent a more important factor determining the growth of bigger seedlings, when the energy stored in the cotyledons becomes completely exhausted (Zagt 1997). In the present study only small seedlings were selected. The initial reserves in their cotyledons might well have played a determinant role in their growth.

## Conclusion

Our descriptive and experimental study of the effect of flooding on the performance of seedlings in a low floodplain of the Mata-Mata River provided evidence that seedling growth of *Mabea nitida* was not affected by flooding. Seedlings of *Pouteria* and *Eschweilera* showed a reduced growth when completely submerged by floodwater. Seedlings of *Pouteria* and *M. nitida* with more leaves showed a faster growth. Flooding reduced the attacks by spiders and fungi on seedlings from all species, and reduced herbivory on seedlings from *Pouteria*. Thus our results do not yield support to the idea that flooding would increase the negative impact of pathogens or herbivory on the growth of seedlings. Any influence from soil nutrient availability or canopy openness on seedling growth was not detected.

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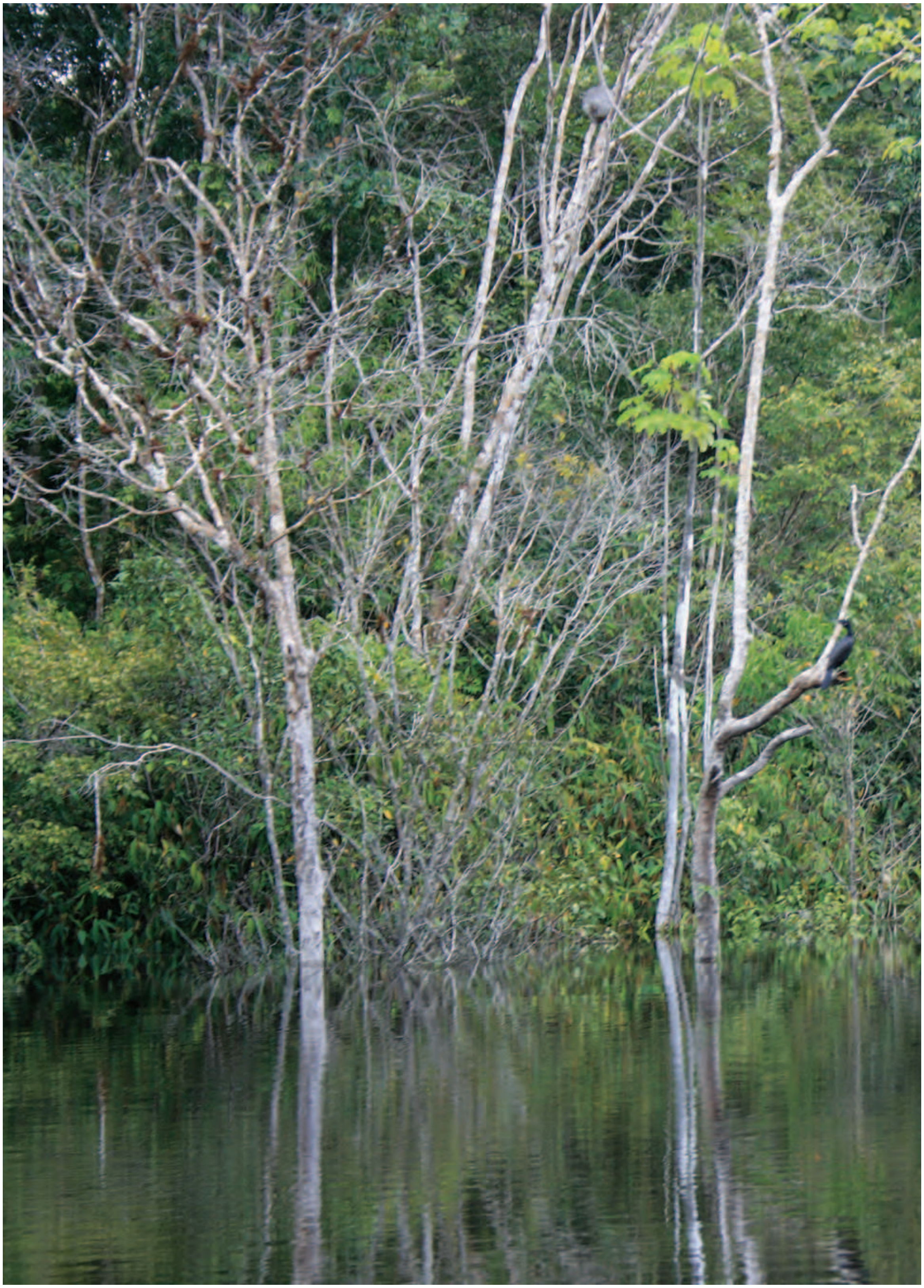

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