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Floodplain and upland populations of Amazonian *Himatanthus sucuuba*: Effects of flooding on germination, seedling growth and mortality

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Abstract

Himatanthus sucuuba is a tree species that occurs in Central Amazonian white water floodplains and in non-flooded uplands. The objective of this paper was to verify whether flooding causes differences in germination percentages, seedling mortality as well as alterations of leaf number and biomass increments, related to the habitat of origin of the seeds (várzea floodplain versus terra firme upland, in the following V and TF, respectively). To test this effect, seeds from populations of both habitats were collected, and germination percentages were calculated under different experimental conditions. One hundred seeds collected in three sites of the floodplain and one hundred seeds from three sites of the upland were placed in trays for germination in a greenhouse in the Amazon Research Institute (INPA) in Manaus, Brazil. Seedlings with a height of 7 cm were then subjected to a period of 120 days of flooding in tanks with three treatments: control, waterlogging (root system and the base of the stem), and complete submersion. Ground water from the INPA was used in the tanks and was changed at weekly intervals. Germination percentages were high in most treatments. Seedling mortality was significantly higher in seedlings originating from upland, reaching 100% in submerged seedlings. On the other hand, várzea-originated seedlings showed no mortality under waterlogging or submergence.

Height growth of waterlogged seedlings from floodplains exceeded that of the control. Submerged seedlings did not grow, independently of the origin, and those originating from uplands died after about 100 days. Number of leaves and leaf area were significantly lower under partial submersion than in the control, independently of the origin of the seeds. Under total submersion abscission of all leaves was verified 30 days after inundation for seedlings of both origins. In the V population, all seedlings survived the waterlogged period, whereas in the TF population, 30% of the seedlings died when subjected to waterlogging. With complete submergence, in the V population 30% of the seedlings had died after 120 days, in the TF population after 90 days mortality was 100%. The results show that germination, seedling growth and seedling survival in *H. sucuuba* differ among populations of floodplain and upland sites: V plants performed better than TF plants under waterlogging and under submersion. The results strongly indicate that ecotypic differentiation exists between these two populations of *H. sucuuba* individuals in the two habitat types, which may be enforced by a strong selective pressure due to the regular occurring flood pulse.

1. Introduction

Trees of Central Amazonian floodplain forests are subjected to annual periods of flooding which last up to 210 days (Junk, 1989). The mean flooding amplitude can reach 10 m (Junk, 1989) resulting in the occurrence of an aquatic and a terrestrial period in the annual course (Junk et al., 1989). Under these circumstances, the tree species have to adjust their life cycles to this annual alternating of environmental conditions. The aquatic period causes conditions of waterlogging or even complete submergence for seedlings and adult trees which these have to withstand in order to colonize the floodplains (Piedade et al., 2001). The tolerance to these conditions varies with plant age and the duration of flooding (Kozlowski, 1984; Lytle and Poff, 2004).

Due to the costs for the maintenance of metabolism under hypoxic or even anoxic conditions, the plant species inhabiting floodplains often have low biomass increments during the aquatic phase. The biomass increment is a possible measure to quantify individual growth of plants or groups of plants in a forest (Kozlowski et al., 1991; Crawford, 1992). Among the

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factors which lead to the loss or decrease of biomass production we may cite photosynthetic activity, loss of carbohydrates for respiration, loss of plant parts due to decomposition, and environmental limitations linked to differences in soil quality, temperature and water supply (Kozlowski et al., 1991; Long and Hällgren, 1993; Pezeshki, 2001). Water supply is also closely related to leaf area and consequently to photosynthesis and growth (Kozlowski and Pallardy, 1984; Kozlowski et al., 1991). Since waterlogging affects the functioning of roots (Kozlowski, 1984), not only flooding of the complete plant has a strong effect on its growth but also partial inundation may cause severe growth reductions (Pezeshki, 2001). However, in some adapted species, waterlogging is known to enhance plant growth (Parolin, 2001).

Due to the extreme flooding conditions in Amazonian floodplains, most species are highly adapted (Parolin et al., 2004) and many are confined to this particular habitat. However, some species occur over a large range of environmental conditions; in fact, an estimated 20% (Piedade et al., 2001) of the tree species common to Amazonian floodplains grow also in the adjacent non-flooded terra firme forests. Here the question arises whether individuals from different habitats respond differently when subjected to extreme flooding conditions.

We chose *Himatanthus sucuuba* (Apocynaceae) as the study species since it occurs both in floodplains (várzea, sensu Prance, 1979) and uplands (terra firme). It is also a tree of high local economic importance, especially for the known phytotherapic value of its latex which in popular medicine is indicated for the treatment of fractures as well as rheumatic and gastric problems (Van Den Berg, 1984).

The present paper focuses on the following question: are there differences of flooding tolerance in different populations of one species, *H. sucuuba*, growing in the várzea floodplain (V) and in the non-flooded terra firme (TF)?

For this purpose, we determined the influence of different flooding regimes (partial, complete submergence) on seedlings using mortality, leaf number, leaf area and biomass increment as indicators to compare the performance of seedlings originating from populations of the two habitats, floodplains and uplands.

We expect that different selective pressures act in the two environments, selecting for different tolerances and perhaps adaptations to cope with flooding. By understanding the adaptive mechanisms of the plants in different habitats we will gain some knowledge about their limits of tolerance to environmental factors, particularly in the seedling phase, which is critical for establishment (Junk, 1993). The seedling stage is the most susceptible to environmental changes (Kozlowski, 1984) and particularly in floodplains it corresponds to the period of highest losses of individuals in a population (Piedade et al., 2000).

2. Material and methods

2.1. Plant material

Himatanthus sucuuba (Spruce) Wood., Apocynaceae, is an arboreal latescent tree ranging from 8 to 20 m of height. The species is allogamous and pollination is performed by insects of the Sphingidae family (Plumel, 1991). The floral biology of
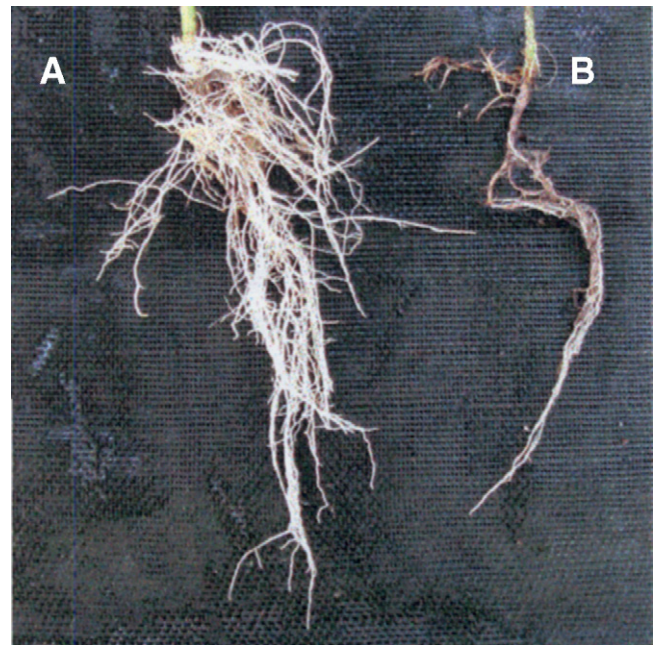

Fig. 1. Root architecture formed in waterlogged seedlings originating from V (A) and TF (B) after 120 days of flooding. Seedling age was 3 months.

the species has not been studied yet, and there are no details on the pollination process of the plant except that a moss (Sphyngidae) is known as visiting the species. Reproduction is annual, by seeds; fruits are dehiscent with several ellipsoidal dry seeds, totally recovered by a well developed circular wing membrane (Fig. 1) which facilitates the seed dispersal both, by wind (anemochory, Plumel, 1991), and water (hydrochory, Ferreira et al., 2005). The genus is mainly distributed within the Amazon Basin (Plumel, 1991). In regions surrounding the city of Manaus *H. sucuuba* is frequently found in várzea areas where the plants may remain under continuous inundation up to 5 months (Wittmann et al., 2002), and at the terra firme in slops and advanced successional stages (Ribeiro et al., 1999), where there is no waterlogging. In both places the species occupy forest edges in places with high light intensity. The plant life span is estimated at 60 years (J. Schoengart, unpublished data).

2.2. Experimental site

The experiment was performed in a greenhouse in the Amazon Research Institute (INPA) in Manaus, Brazil, at the INPA/Max-Planck Project.

All sites of collection were close to Manaus, Central Amazonia: várzea (V) sites were located on the Ilha de Marchantaria ($03°15'S$, $60°00'W$) and the terra firme (TF) sites in the Reserva Florestal Adolpho Ducke ($02°53'S$, $59°58'W$). The distance in a straight line between the sites is of about 40 km of a landscape composed by patches of the city of Manaus, and the Amazonas/Solimões River.

Seedlings were grown from seeds collected in their natural environments. In order to avoid collecting plants generated from one single parent seeds were collected in three sites per environment (V and TF) about 1 km far apart from each other. Mature

fruits were collected from mother plants at the three sites in the várzea (V) and three sites at terra firme (TF) and transported to the INPA, Manaus. Fruits were subsequently placed in the sun to help opening and release of the seeds. Opening took place in a maximum period of 3 days. After being released, seeds from the three sites in each environment were mixed in order to obtain one single lot for V and one single lot for TF. No particular storage procedure was used for seeds since they were used within 3 days of release.

One hundred seeds from V and one hundred seeds from TF were disinfected surface sterilized with sodium hypochlorite 10% for 15 min and washed in tap water. Then, the wing-like involucres were mechanically removed (Ferreira et al., 2005) and seeds were placed in trays (20 cm × 60 cm) for germination at ambient temperature (medium value of 28 °C). Two different neutral substrates were used: sand + sawdust (1:1), and sand + sawdust (1:1) + water; seeds were submerged in a water column of 5 cm. Germination tests were performed over a 15-day period. Germination was defined as the radicule protrusion (1.5 cm) (Burtt, 1991).

Seedlings, 30 days of age and 7 cm in height, were transferred to polyethylene pots (19 cm × 16 cm) (one seedling/pot) containing soil from their native environment. Soil samples were collected both in V and TF from the 20 cm top layer, after removing the superficial litter. This stratum was selected since it is the richer in minerals, owing to the litter decomposition in the TF (Schubart et al., 1984) and by the deposition of newly eroded sediments drift from the Andean by the water currents, during the flooding period in the V (Furch, 1997). Soil was collected in one single location in the V and TF, since previous studies showed that differences between várzea and terra firme soils are much bigger than eventual differences owing to soil microhabitat within the várzea or terra firme (Furch, 1984). "Seedling" was defined as the first year's stage, after seed germination.

For the simulation of flooding events, we used five tanks of 1.5 m × 2.5 m (1000 L) for each treatment, with a total of 15 tanks. Eight seedlings of *H. sucuuba*, 90 days of age (60 days after transplantation), were placed randomly in each tank, four originating from V and four from TF (*n* = 5). At the start of the flooding events seedlings were 3 months old, the average period they remained without flooding in the V habitat, throughout the terrestrial phase.

During 120 days the seedlings were subjected to three hydric conditions that predominate in their environments (Junk et al., 1989): control (well-watered), waterlogged (roots and parts of the stems flooded, water height 25 cm), and submerged (whole plant flooded, water height 70 cm). Ground water from the INPA was used in the tanks and was changed at weekly intervals. The water in the tanks of all treatments did not present algae contamination or further organic matter decomposition (i.e. leaves from outside trees). Conditions in all tanks were identical and the random distribution of the seedlings from different origins ensured the comparability of the results.

All tanks were covered to 70% with a net (SOMBRITE) in order to simulate the natural conditions of light penetration into the water under environmental conditions in the white water of the várzea, where Secchi depths are between 25 and 40 cm (Sioli, 1984).

2.3. Monitored parameters

Height growth was measured at intervals of 2 weeks for 120 days. Leaf number, leaf area, biomass and mortality were analyzed in all treatments when the experiment ended after 120 days. Leaf area was determined with a leaf area meter (LEAF AREA METER, DELTA-T DEVICES), and specific leaf mass was obtained by relating the dry matter of leaves and the leaf area. Biomass (dry mass) was measured after cautiously extracting the seedlings from the pots washing and drying them for about 1 h at ambient temperature and dividing the plants into the categories: roots, stem, leaves and dead material. Dead material was defined as degenerating vegetative material: the leaves that had symptoms of chlorosis on more than 50% of their blade. Total biomass was calculated by summing up the biomass of the mentioned categories. After determining fresh mass, dry mass was taken by drying the material to constant weight in a HERAEUS oven at 95 °C. Every part of the plant was weighed with analytic scale BELMARQ 210 A, 0,0001 g of precision. The differences between treatments of the measured parameters were tested for their significance using Tukey's test with 5% probability.

2.4. Statistical analyses

Seed germination and survival: Each tray was assumed as one replicate. Tests were made over a basis of four repetitions of 100 seeds each, per treatment.

Seedlings growth and survival: two origins (V and TF) × three flooding treatments × five tanks (replicates). Four plants per origin were placed per tank, in a total of eight plants in a randomized design. ANOVA was used to establish variance and the comparison between medium values used Tukey's test at 5% of probability. Statistical analyses were performed in Systat 8.0.

3. Results

3.1. Germination

Germination percentages varied according to the substrate and the seed's origin (V or TF; Table 1): in sand + sawdust germination was 91% (TF) and 94% (V) with no significant difference.

Table 1
Germination percentages (%) and survival of seedlings after the first year (%) of *H. sucuuba*, from the V (várzea) and TF (terra firme) environments

Habitat	Germination (%)		Seedlings (%)	
	Sand + sawdust	Water	Sand + sawdust	Water
V	94 (±2.6) A	98 (±1.7) A	94 (±1.7) A	84 (±2.9) A
TF	91 (±0.8) A	64 (±1.0) B	91 (±2.1) A	0 B

Numbers followed by equal letters in the columns have no statistical differences (Tukey 5%), *n* = 100.

Table 2
Means and standard deviation of plant height, number of leaves (LN), total leaf area (LA), area and mass of a single leaf and specific leaf mass (mg/cm^2) of *H. sucuuba* in response to 120 days of waterlogging

	Control		Waterlogging	
	V	TF	V	TF
Plant height (cm)	47.8 (±4.1) A	16.9 (±2.8) B	45.7 (±3.6) A	18.5 (±2.6) B
Number of leaves	11.0 (±0.8) A	6.0 (±0.8) B	7.0 (±0.5) B	5.0 (±0.8) B
Total leaf area (cm^2)	53.0 (±1.9) A	27.9 (±1.1) B	10.8 (±5.4) a	7.8 (±1.1) a
Leaf area (cm^2)	4.8 (±0.2) A	4.7 (±0.6) A	1.5 (±0.8) a	1.6 (±0.3) a
Leaf dry mass (mg)	14.3 (±0.5) A	19.5 (±2.9) B	5.3 (±2.0) a	5.1 (±1.3) a
Specific leaf mass	2.9 (±0.04) A	4.2 (±0.7) B	4.6 (±0.2) B	3.2 (±0.8) A

Numbers followed by equal letters in the row have no statistical differences (Tukey 5%), *n* = 5.

In water, where the seeds sank after removal of the wing-like involucres, germination was significantly different with 64% (TF) and 98% (V).

3.2. Height growth

All seedlings of V showed higher height growth than those from TF. In the seedlings from TF, height growth of waterlogged seedlings exceeded that of the control, whereas in those from V the control seedlings were slightly higher (see Table 2). Submerged seedlings did not grow, independently of the origin, and in those originating from TF they died after about 100 days.

3.3. Number of leaves, leaf area and biomass

When subjected to complete submersion, the seedlings of *H. sucuuba* of both environments V and TF lost 100% of their leaves within a maximum period of 30 days. In the waterlogged and in the non-flooded control treatments seedlings kept their leaves during the 120 days of the experiment, independent of their origin. The number of leaves, however, was higher at the end of the experimental period in the V-Control (see Table 2). However, the reduction in the number of leaves in the flooded treatment was much less pronounced than in the seedlings from TF.

Leaf area in the V-Control was about two times higher than the TF-Control (Table 2). In the waterlogging treatment, values of leaf area were comparatively modest (about five times smaller than the V-Control) and the differences between V and TF under waterlogging were not significant (Table 2).

In the control treatment, leaves from the TF were heavier than those from the V (Table 2). However, this response was

not found when seedlings were subjected to waterlogging. On the other hand, seedlings of the V at the waterlogging treatment showed a significant increase in the values of specific leaf mass, while an opposite pattern was obtained in TF, where significant reductions were achieved (Table 2).

Initial total biomass was higher in V seedlings than in TF seedlings (7.8 versus 2.5 g, Table 3). With waterlogging, seedlings originating from V had 57% lower total biomass than the control seedlings (Table 3). Those subjected to submergence had a decrease of 67%, with the complete loss of leaves being responsible for most of the reduction. Seedlings originating from the TF subjected to waterlogging had 44% lower total biomass than the control seedlings (Table 3); those subjected to submergence were all dead after 120 days. Seedlings subjected to waterlogging over a 120 days period showed a significant increase in the ratio root/aerial part, both in the TF and V populations (Table 3). The same was obtained for the seedlings from the V that survived throughout the total submersion period.

Leaf dry mass was lower in seedlings subjected to waterlogging than in those of the control (Table 3). In the V-Control stems were responsible by representing ca. 50% of the produced biomass while in the TF-Control, leaves comprised had a higher percentage of total biomass. Under waterlogging, higher biomass than in the control was allocated to the roots in both, V and TF origins, although it was comparatively more in V seedlings as was indicated by the root/shoot ratio (Fig. 1).

3.4. Survival

In the well-watered control, the survival rate was 100% for both V and TF. With partial flooding (waterlogging), the V pop-

Table 3
Mean biomass of different plant parts (g), followed by standard deviation, in *H. sucuuba* after 120 days with different flooding regimes

	Control		Waterlogging		Submergence	
	V	TF	V	TF	V	TF
Roots	2.4 (±0.5) A	0.5 (±0.6) B	1.5 (±0.5) B	0.7 (±0.1) B	0.4 (±0.1) B	0
Stem	3.7 (±0.5) A	0.8 (±0.1) B	1.4 (±0.3) a	0.6 (±0.1) B	0.6 (±0.1) B	0
Leaves	1.7 (±0.2) A	1.0 (±0.2) B	0.4 (±0.1) a	0.2 (±0.2) a	0	0
Dead material	0.1 (±0.1) A	0.1 (±0.1) A	0.1 (±0.1) A	0.1 (±0.1) A	0	0.3 (±0.1) B
Total	7.8 (±0.9) A	2.5 (±0.3) B	3.3 (±0.5) a	1.7 (±0.3) b	1.1 (±0.1) C	0.3 (±0.1) c
Root:shoot ratio	0.4 (±0.1) A	0.2 (±0.1) B	0.9 (±0.3) a	0.8 (±0.2) a	0.6 (±0.2) A	0

Numbers followed by equal letters in the row have no statistical differences (Tukey 5%), *n* = 5.
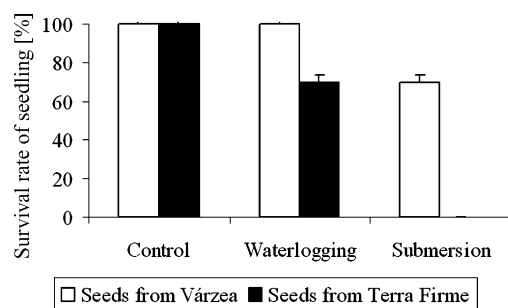
Fig. 2. Survival percentage of seedlings originating from seeds of V and TF under waterlogging and submersion, with standard deviation (number of replicates *n* = 5) after 120 days of flooding.

ulation showed lower mortality than the TF population: in the V population, all seedlings survived the waterlogged period, whereas in the TF population, 30% of the seedlings died when subjected to waterlogging.

With complete submergence, in the V population 30% of the seedlings had died after 120 days, in the TF population after 90 days mortality was 100%. In these seedlings, first the roots began to rot, and then the plants died (Fig. 2).

4. Discussion

The seeds and seedlings from the two habitat types differed in their tolerance to flooding. The V populations analysed in this study were more tolerant to waterlogging than the TF populations, which became evident by the higher germination rate, coupled to the increased capacity to grow quickly under waterlogged conditions and to preserve their root systems.

Only in seeds from the V seedlings emerged after germination in the water. In fact, the number of species germinating under hypoxic or anoxic conditions is low (Frankland et al., 1987; Crawford, 1992). Few terra firme trees are able to germinate under anoxic conditions, and also in Amazonian várzea it is seldom found in the several hundred tree species endemic to this environment. Some examples of species where germination under water was documented in várzea trees are *Inga affinis* and *Sesbania virgata* (Lobo and Joly, 1998), *Carapa guianensis* (Scarano et al., 2003), *Mora paraensis*, *Vatairea guianensis*, *Crateva benthami*, *Nectandra amazonum* (Parolin and Junk, 2002), and *Salix martiana* (Oliveira and Piedade, 2002).

The rotting of the radicule in the seeds of *H. sucuuba* germinating in water may be related to the accumulation of toxic compounds of the anaerobic metabolism (Ferreira, 2002). Since the majority of the V seeds formed healthy seedlings (84%), we may suppose that the V population has efficient mechanisms of removal or tolerance of toxic compounds, as suggested by the formation of aerenchyma and lenticels (Ferreira et al., 2005).

Seedlings from the V subjected to waterlogging grew as much as those of the control, with medium growth values superior to the seedlings from TF under the same treatment. This difference in the growth characteristics may indicate dissimilar adaptation among the two populations, suggesting that seedlings from V may follow the escape strategy (Parolin, 2003), which consists in performing a faster growth in order to keep the photosynthe-

sizing leaves above the water as long as possible, ensuring the maintenance of a better energetic balance. On the other hand, growth disruption in seedlings from both the V and TF populations under total submersion may be a strategy to cope with the heavy costs of the anaerobic metabolism (Crawford, 1992). Usually the metabolic rates are reduced to energetic levels only sufficient to allow the survival of the roots, thus ensuring the seedling's survival until the next water receding event.

The seedlings from V formed approximately twice as many leaves as the seedlings from TF, but they had the same average leaf area and lower leaf dry mass. Although leaf number in the control was significantly higher, almost twice the value of the TF control, the ratio leaf area/leaf number showed that leaf area was the same. Leaves from TF may concentrate more structural tissues in comparison to leaves from V, since they are heavier, suggesting a different partitioning and allocation of biomass, possibly triggered by environmental constraints since it is well known that in aquatic habitats, structural tissues tend to be reduced (Sculthorpe, 1985).

The reduction in number of leaves and the increase of the specific leaf mass in seedlings from V after flooding is a typical characteristic related to xeromorphic leaves (Fahn and Cutler, 1992). This might indicate that, however although in an aquatic environment, water shortening may take place for plants, resulting in a physiologic drought (Kozlowski, 1997), as root modifications related to oxygen shortage will compromise their functionality (Ferreira, 2002). Xeromorphic leaves have been reported already for several Amazonian floodplain trees (Waldhoff and Furch, 2002), specially in periods of extremely high water level, when only the crown of several trees remain above the water surface. Seedlings from the TF population did not show such a trend. Additionally, both V and TF populations increased the ratio root/aerial part, and again, the priority in terms of energetic balance favors the root system, another typical response of plants under water deficiency (Kozlowski et al., 1991).

All in all, seedlings from V exhibited adaptations to the flood that allowed them to perform better than those from TF. The latter ones died up to 90 days after submergence. These different results shown in the two populations, together with differences measured in ADH quantity produced (Ferreira et al., 2005), indicate a wider range of flooding tolerance in the V population. These results strongly indicate that ecotypic differentiation exists between these two populations of *H. sucuuba* individuals in the two habitat types, which may be enforced by a strong selective pressure due to the regular occurring flood pulse.

Concluding, *H. sucuuba* is a species which is highly tolerant of waterlogging. Still, the experimental treatments of waterlogging and submergence showed that seedlings resulting from seeds collected in the V floodplain had a higher tolerance to waterlogging and an extremely higher tolerance to submergence than had the seedlings resulting from seeds originating in the non-flooded uplands. It may be supposed that the populations in the different environments are separating, and the V population has developed further adaptations which enable the seedlings to survive the periods of extreme flooding which the plants in this environment are subjected to at regular intervals. They probably

possess diversified mechanisms of adaptations which compensate for the injuries caused by the long periods of uninterrupted water excess as are typical for the trees growing in these environments (Parolin et al., 2004). These adaptations may involve morpho-anatomical or physiological adaptations as strategies for survival.

Although somewhat speculative at this stage, it appears that there are two types of cases: First, plants with a broad range of occurrence in flooded and unflooded habitats, such as the one studied here or e.g. in *Carapa guianensis* (Scarano et al., 1994, 2003) or other species (Kubitzki and Ziburski, 1994). Second, plants where speciation may have already taken place (e.g., the genera *Dalbergia*, *Parkia*, *Tabebuia*; Scarano and Crawford, 1992; Cordero and Molano-Flores, 1996; Ribeiro et al., 1998). In the case studied here, it would appear that 1 is a step toward 2. For some other species (e.g., perhaps, *Carapa guianensis*) this may not be so. Studies of plant establishment *in situ* are needed to give insight into these open questions.

Acknowledgments

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