

Flood-tolerance and flood-escape mechanisms for seeds and seedlings of common swamp trees of Central America

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Abstract: Tropical swamp forests are characterized by relatively low diversity of tree species which are often believed to be flood tolerant. However, the diverse habitats in which some “swamp” species, e.g. *Callophyllum brasiliense*, are found suggest that the trees may not be uniquely adapted to swamp living. I conducted a series of experiments on seeds and seedlings of common Central American swamp forest trees. In total, eleven species were used in different germination and seedling survival experiments. The refuge provided by *Pterocarpus officinalis* buttresses was explored in two short studies. Germination experiments in the field indicated that seeds of some swamp species (notably *Callophyllum brasiliense*, *Carapa guianensis*, and *Prioria copaifera*) did not germinate in standing water, and similarly did not survive six-week periods of submersion as seedlings. In a microtopography study, overall seedling densities were significantly higher in the elevated refuge provided by *Pterocarpus* buttresses. In the absence of adaptations to flooding, other mechanisms might be important in allowing the establishment and survival of tree species in swamps. Together, the results suggest that although flood tolerance is strong in some species, flood escape may be the method by which other common species establish in swamps. Key species like *Callophyllum brasiliense*, *Carapa guianensis* and *Prioria copaifera* are not flood tolerant but instead utilize a range of flood escape mechanisms to allow their existence in swamp forests.

Resumen: Los bosques tropicales de pantano se caracterizan por tener una diversidad de especies arbóreas relativamente baja, de las cuales por lo general se piensa que son tolerantes a la inundación. Sin embargo, los diversos hábitats en los que se encuentran algunas especies “de pantano”, e.g. *Callophyllum brasiliense*, sugieren que los árboles podrían no estar adaptados únicamente a la vida en el pantano. Llevé a cabo una serie de experimentos con semillas y plántulas de árboles de pantano comunes de América Central. En total se usaron 11 especies en diferentes experimentos de germinación y supervivencia de plántulas. El refugio proporcionado por los contrafuertes de *Pterocarpus officinalis* fue explorado en dos estudios cortos. Los experimentos de germinación en el campo indicaron que las semillas de algunas especies de pantano (notablemente *Callophyllum brasiliense*, *Carapa guianensis* y *Prioria copaifera*) no germinaron en agua estancada y que las plántulas no sobrevivieron a periodos de seis semanas en los que estuvieron sumergidas. En un estudio de la microtopografía, las densidades generales de plántulas fueron significativamente mayores en el refugio elevado proporcionado por los contrafuertes de *Pterocarpus*. En ausencia de adaptaciones a la inundación, otros mecanismos podrían ser importantes para permitir el establecimiento y la supervivencia de especies arbóreas en los pantanos. En conjunto, los resultados sugieren que si bien la tolerancia a la inundación es grande en algunas especies, el escape a la inundación puede ser el método por el cual otras especies comunes se establecen en los pantanos. Especies clave como *Callophyllum brasiliense*, *Carapa guianensis* y *Prioria copaifera* no son tolerantes a la inundación, sino que por el contrario utilizan una gama de mecanismos de escape a la inundación que les permiten existir en los bosques de pantano.

Resumo: As florestas tropicais dos pântanos são caracterizadas pela relativamente baixa diversidade arbórea e cujas espécies são frequentemente julgadas tolerantes à inundação. Contudo, a diversi-

dade de hábitos nas quais algumas espécies, e.g. *Callophyllum brasiliense*, são encontradas, sugere que as árvores podem não estar simplesmente adaptadas a viver nos pântanos. Neste contexto, um conjunto de experiências foi efectuado em sementes e plântulas de espécies arbóreas comuns nos pântanos da América Central. No conjunto foram estudadas onze espécies sujeitas a ensaios de germinação e sobrevivência. O refúgio proporcionado pelos contrafortes basais da *Pterocarpus officinalis* foi explorado em dois pequenos estudos. As experiências de germinação no campo indicaram que as sementes de algumas espécies do pântano (principalmente a *Callophyllum brasiliense*, *Carapa guianensis* e *Prioria copaifera*) não germinam em águas paradas, e igualmente, as suas plântulas não sobrevivem a um período continuado de seis semanas em submersão. Num estudo microtopográfico, verificou-se que as densidades globais das plântulas foram significativamente mais elevadas nas zonas de refúgio mais elevadas providenciadas pelos contrafortes basais dos *Pterocarpus*. Na ausência de adaptações ao alagamento, outros mecanismos poderão ser importantes na viabilização do estabelecimento e sobrevivência das espécies lenhosas nos pântanos. Em conjunto, os resultados sugerem que embora a tolerância ao alagamento seja forte em algumas espécies, a defesa ao alagamento pode ser o método pela qual outras espécies comuns se estabelecem nos pântanos. Árvores referência como a *Callophyllum brasiliense*, *Carapa guianensis* e *Prioria copaifera* não são tolerantes ao alagamento mas, pelo contrário, utilizam um conjunto de mecanismos de defesa para permitir a sua existência nas florestas dos pântanos.

Key words: Swamp trees, seed germination, seedling submersion, flood tolerance, flood escape.

Introduction

Periodic and seasonal flooding of tropical swamp forests generates stress among the tree species that live there (Lopez & Kursar 2003; McHargue & Hartshorn 1983b). Adult trees live with their roots submerged nearly all of the time, and seeds and seedlings must survive, germinate, and grow under the stress of floating or being submerged intermittently. Flood tolerance is of obvious importance for a swamp species.

The extreme of flood tolerance in tropical trees is found in the Igapó and Várzea forests of the Amazon basin (Fernandes-Correa & Furch 1992; Kubitzki & Ziburski 1994), where trees are covered by as much as 7 m of water that flood the forests for up to 300 days a year (Schluter *et al.* 1993). In Central American swamp forests (forests with soils permanently saturated by fresh water), shorter periods of inundation and shallower flooding are more the norm (Lopez 2001; Urquhart 1997). While some areas have permanent standing water, most Central American swamps have annual, periodic flooding, with periods of high water lasting from a few days to several months. In Eastern Nicaragua, flood waters rise to 20-40 cm depth for the 8 month rainy season (May-December), and often rise significantly higher for periods of three

to six weeks during the wettest parts of the rainy season. In the swamp forests of Eastern Nicaragua, common tree species differ in aspects of fruiting period, seed size and seed dispersal (Urquhart 1997), yet they all face the stress of flooding. In this diverse assemblage of species, it is likely that many mechanisms are employed as trees cope with periodic flooding.

Under the general hypothesis that swamp species utilize various mechanisms that allow them to cope with seasonal flooding, I conducted experiments on the abilities of several common swamp tree species to cope with flooding as seeds and seedlings. I investigated the ability of seeds to germinate while in standing water, along with the ability of seedlings to survive periods of submersion similar to those experienced during flood periods. I also conducted field studies in the swamps of Nicaragua, on the relationship between seedling density and microtopographical features, e.g. the elevated sites produced by *Pterocarpus officinalis* Jacq. (Fabaceae) buttresses, which allow seeds and seedlings to perch above the water.

Seed germination trials tested the hypothesis that the ability to germinate in standing water is not universal among swamp species. The predictions of this hypothesis are that individual species would germinate better under certain conditions

(in standing water vs. perched) and that within a particular condition there would be differences in germination success among species. The experiments on seedling submersion, mostly conducted at the University of Michigan Matthai Botanical Gardens, tested the hypotheses: (1) that the length of submersion affects seedling survival, and (2) species vary in their ability to survive submersion. If the first hypothesis is true, species should show differential survival, growth, and leaf production among different periods of submersion. If the second is true, for a given period of submersion, there would be differences among species in survival, growth, and leaf production. In the microtopography study, I tested the hypothesis that the elevated buttresses of *P. officinalis* provide refuge from flooding for seedlings, thus seedling density would be dependent upon distance from a *P. officinalis* tree, with more seedlings on the buttress platform (near the tree) and fewer off the platform (away from the tree).

Materials and methods

Description of swamp forests at primary field site

The field portion of this work was done in the Caño Negro area outside of Bluefields, Nicaragua. Swamp forests are defined here as forested freshwater ecosystems with permanently saturated soils. The swamp forests of this area are characterized by low diversity (< 20 spp ha⁻¹) with the most common species in approximate order of abundance being *Raphia taedigera* Mart. (Arecaceae), *Pterocarpus officinalis* Jacq. (Fabaceae), *Carapa guianensis* Aubl. (Meliaceae), *Grias cauliflora* L. (Lecithydaceae), *Calophyllum brasiliense* Cambess. (Clusiaceae) and *Symphonia globulifera* L.f. (Clusiaceae). The forests are a large plain (~50,000 ha) drained by Caño Negro and Kukra River to the south. The swamp soils are typically thick peat (up to 3-4 m depth, Urquhart 1999). This region has a dry season with little rain falling during January-April, and receiving the bulk of its 3000 mm of precipitation from May-December (Urquhart 1997). With the exception of dry El Niño years, in most locations the soils are covered with 20-40 cm of water during the wet season, with deeper flooding occurring for periods of up to six weeks during peak rains of July, August, October and November. Flood water levels of 1 m or

more depth for as long as six weeks caused by heavy rains are reported to occur on a nearly annual basis (E. Lemos, pers. comm.). Along the riverbanks of these swamps, *Pachira aquatica* Aubl. (Bombacaceae), *Lonchocarpus costaricensis* Pittier (Fabaceae), *Andira inermis* H.B.K. (Fabaceae), *Posoqueria latifolia* Roem. & Schult. (Rubiaceae), *Annona glabra* L. (Annonaceae) and *Rhizophora mangle* L. (Rhizophoraceae) are common cohabitants with the aforementioned species. The Red Mangrove (*Rhizophora*) occurs along sections of the river that have low salinity during the dry season and are entirely freshwater during the wet season, and is hence included in some sections of this study.

Seed sources

I harvested seeds of *Prioria copaifera* Griseb. (Caesalpinaceae) and *Raphia taedigera* from roadside swamps along the highway running from Puerto Limon to Puerto Viejo on the Atlantic Coast of Costa Rica. At the same time, T. Webb and R. Peralta of Portico, S. A. provided me with seeds of *Carapa guianensis* from the forests around Cariari, Heredia, Costa Rica and I received seeds of *Calophyllum brasiliense* from FUNDECOR in Puerto Viejo, Heredia, Costa Rica. In early August 1994, I collected seeds from *Pachira aquatica*, *Lonchocarpus costaricensis*, *Grias cauliflora* and *P. officinalis* trees on the banks of Caño Negro, near Bluefields, Nicaragua. In importing the seeds to the United States, *P. officinalis*, *P. copaifera* and *C. brasiliense* seeds failed United States Department of Agriculture (USDA) inspection and were destroyed. To replace the destroyed seeds, I received seeds of *C. brasiliense* and *P. officinalis* from Puerto Rico. The *C. brasiliense* seeds came from roadside ornamental trees, whereas the *P. officinalis* seeds were from freshwater swamps. I collected seeds of *P. officinalis*, *Andira inermis*, *Posoqueria latifolia*, and *Annona glabra*, as well as propagules of *Rhizophora mangle* from trees along Caño Negro in Nicaragua. The *A. inermis* and *P. latifolia* that served as seed sources were growing in *terra firme* forests, although they are both found in swamps (Allen 1956; Beach 1983; Urquhart pers. obs.). I was unable to collect seeds of *Symphonia globulifera*, a common tree of the swamps of Eastern Nicaragua, and hence it was omitted from the study. Table 1 lists the seed sources for the species used in the experiment.

Table 1. Seed sources for experiments. Details are given in the text.

Species	Family	Germination experiment seed source	Collected	Submersion experiment seed source	Collected
<i>Andira inermis</i> H.B.K.	Fabaceae	–	–	Nicaragua	Oct 95
<i>Annona glabra</i> L.	Annonaceae	–	–	Nicaragua	Oct 95
<i>Calophyllum brasiliense</i> Cambess.	Clusiaceae	Costa Rica	Jul 93	Puerto Rico	Dec 93
<i>Carapa guianensis</i> Aubl.	Meliaceae	Costa Rica	Jul 93	Costa Rica	Jul 93
<i>Grias cauliflora</i> L.	Lecithydaceae	Nicaragua	Aug 93	Nicaragua	Aug 93
<i>Lonchocarpus costaricensis</i> Pittier	Fabaceae	Nicaragua	Aug 93	Nicaragua	Aug 93
<i>Pachira aquatica</i> Aubl.	Bombacaceae	Nicaragua	Aug 93	Nicaragua	Aug 93
<i>Posoqueria latifolia</i> Roem. & Schult.	Rubiaceae	–	–	Nicaragua	Oct 95
<i>Prioria copaifera</i> Griseb.	Caesalpinaceae	Costa Rica	Jul 93	–	–
<i>Pterocarpus officinalis</i> Jacq. (PR)	Fabaceae	Puerto Rico	Dec 93	Puerto Rico	Dec 93
<i>Pterocarpus officinalis</i> (N)	Fabaceae	–	–	Nicaragua	Oct 95
<i>Raphia taedigera</i> Mart.	Arecaceae	Costa Rica	Jul 93	–	–
<i>Rhizophora mangle</i> L.	Rhizophoraceae	–	–	Nicaragua	Oct 95

I transported all the seeds in moist, air-permeable plastic bags to either the field site in Nicaragua or to the Matthai Botanical Gardens (UMMBG) at the University of Michigan. The research greenhouse at the UMMBG has high humidity and stable, warm temperatures, mimicking the conditions of a tropical forest (Rankin 1978). Lighting is not controlled in the greenhouse and is provided entirely by the ambient sunlight of 42° N latitude. This does not mimic tropical sun, but given that all of these species grow as seedlings under a closed forest canopy (Urquhart 1997 and Urquhart, pers. obs.), light limitation is not a factor.

Seed germination

For field experiments on germination of seeds in standing water vs. perched, I used the seeds from seven species of swamp forest trees: *C. brasiliense*, *C. guianensis*, *G. cauliflora*, *L. costaricensis*, *P. aquatica*, *P. copaifera* and *R. taedigera*. I placed the seeds in seed cages at flooded and perched sites in the swamp forest to the south of Cooperativa La Union, located 15 km up Caño Negro from the town of Blueifields, on the Caribbean Coast of Nicaragua. The seed cages were cylinders made from 1 cm “hardware cloth” (galvanized screen with 1 cm square holes) of roughly 40 cm diameter by 50 cm height. The perched cages had both tops and bottoms of hardware cloth, whereas the sub-

merged cages had no bottom because the open bottoms were pushed into the mud for anchoring. I filled the perched cages with a shallow layer of leaf litter collected from the exposed buttressed roots of *P. officinalis* trees and anchored them to the buttress platform. I located the “wet” treatment cages in standing water, which was approximately 10 cm deep in August. Each cage contained four seeds per species. There were eight replicates of each treatment, for a total of 32 seeds per species per treatment. The experiment began August 15, 1994 and I scored germination on April 18, 1995 (eight months).

For statistical analyses of the data, I used several tests on arcsine-transformed percentages of germination. To determine within species differences in germination between the two conditions, I performed seven separate two-sided Student's *t* tests. Because these tests were for *a priori* hypotheses, I did not adjust significance levels for these tests, using $\alpha = 0.05$ as in all further statistics. For multiple comparisons of species that germinated in water, I performed an ANOVA and Tukey HSD multiple, using $\alpha = 0.05$. Similarly, I excluded the species that failed to germinate when perched and ran an ANOVA and Tukey HSD for the remaining species.

Upon receiving the *P. officinalis* seeds from Puerto Rico, I conducted germination trials at the UMMBG by placing seeds in pots of standing wa-

ter or wet soil. There were a total of 60 seeds/treatment, divided into three replicates of 20 seeds per treatment. I scored germination at 90 days. I used an ANOVA to examine differences in germination percentages.

Seedling submersion

For seedling submersion experiments, I submerged established seedlings that were germinated on saturated Sunshine #1 mix at the UMMBG. After germination and growth to 10-20 cm height, I transferred the seedlings to 10 cm diameter pots with the same substrate and gave them a recovery period of at least 21 days before submersion.

To study the effects of submersion on seedling survivorship, I placed seedlings in submersion tanks for periods of 0, 7, 21 or 42 days. The eight submersion tanks used were 36-gallon dark green Rubbermaid® trash cans filled with well water. *C. guianensis* and *P. aquatica* grew rapidly and were quickly large enough for the submersion experiments. I used one seedling per treatment [0 (control), 7, 21, or 42 days submersion] per species, replicated eight times for a total of eight seedlings per species per treatment. The experiments began on May 7, 1995. After a seedling had finished its submersion period, I removed it from the tank and placed it in a tray beside the tank, where the controls spent the entire experimental period. I measured the height and number of leaves of the seedlings before the experiment and measured height and number of leaves and scored survivorship at 56 days after the beginning of the experiment.

After the completion of the *C. guianensis*-*P. aquatica* submersion experiment, I used the other available species, *C. brasiliense*, *G. cauliflora*, *L. costaricensis* and *P. officinalis*, in a similar experiment, with most replicated eight times for a total of eight seedlings per species per treatment. However, I only had 16 *Calophyllum* seedling so I restricted it to four replicates of the four treatments. Before the submersion and at 56 days, I measured height of the seedlings and number of leaves and at 56 days I scored survivorship. I included all eight in the 42 day submersion treatment to compare survivorship between perched and floating-germinated seedlings.

In a third run, I included seedlings of *P. officinalis* from Nicaragua, *A. glabra*, *A. inermis* and *P.*

latifolia. For each of these species I had the necessary seedlings to run eight replicates of four treatments. I also included eight seedlings of *R. mangle* in the 42 days submersion treatment in an attempt to gauge the impact of this treatment on a well known submersion-tolerant species.

I standardized change in height (H) and change in leaf number (L) by making them percentages of original values.

$$\%H = 100(H_{56}-H_0)/H_0$$

$$\%L = 100(L_{56}-L_0)/L_0$$

The subscripts refer to day of the experiment on which the variable was measured. Statistical analyses of these experiments proved complicated, because low survivorship of some species in the 42 day treatment made sample sizes small and uneven. Using ANOVAs, I analyzed variation among percent growth and percent change leaf number for all 10 species for the first three treatments combined. I performed similar ANOVAs for percent growth and percent change in leaf number for the seven species with high survivorship (>75%) of the 42 day submersion treatment. For survivorship of seedlings in the 42 day submersion treatment, I prepared a 10 species by 2 outcomes table and performed an Exact test (SPSS extension to larger tables of Fisher's Exact test) for likelihood of the distribution.

In the field, I conducted an experiment with *P. officinalis* seedlings to look at effects of flooding in a more natural setting. I was only able to use *P. officinalis* because it was the only species with enough seedlings available. I collected small (20-50 cm h) seedlings from within the swamp and transplanted them into different conditions. Shade treatments were under the closed swamp forest canopy, whereas sun treatments were in nearby, open areas of swamp and exposed to full sun for a significant portion of the day. The four treatments were standing water in shade, standing water in sun, perched in shade, and perched in sun. Each treatment was replicated four times with 10 seedlings per replicate per treatment, with replicates established such that the four different treatments within a replicate were closer to each other than to other replicates. I scored the number of surviving seedlings at 4 and 12 months after transplant. During this time, the swamps flooded for short periods, which submerged the seedlings placed in standing water. I used an ANOVA to analyze percent survivorship at the two censuses.

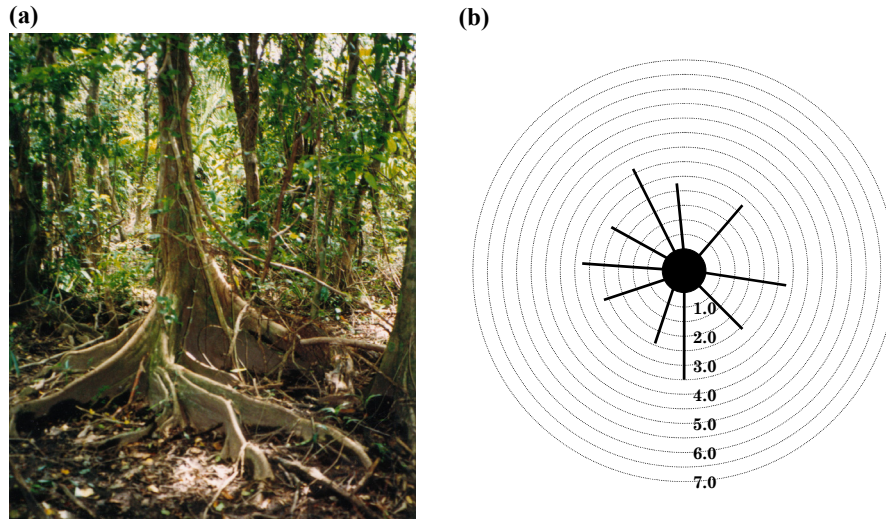


Fig. 1. (a). *Pterocarpus officinalis* Jacq. adult tree with radiating buttresses. Photo taken in swamp in Nicaragua during dry season. (b). Schematic illustration of concentric rounds around *Pterocarpus* trunk used for analysis of seedling densities. Numbers indicate distance in meters from the center of the trunk. Radiating lines are meant to suggest the radiating buttresses.

Microtopographic studies

Because some swamp species appear to need perched sites for germination, I censused seedlings in the most common elevated region of the swamps—*Pterocarpus officinalis* root buttresses (Fig. 1). The buttresses typically form an elevated "table" of debris of up to 3.5 m in diameter. For six adult *P. officinalis* trees, I identified and counted seedlings in a 7 m radius circle from the estimated center of their trunk, noting distance of the seedlings from the estimated center. After noticing

that adult trees were often found growing on the buttresses, I conducted a rapid survey of adult trees found on the buttresses of 15 *P. officinalis* trees.

In the analyses of the seedling data, I grouped species because there were not enough seedlings of any one species for individual analysis. I calculated counts of seedlings in 0.5 m width rings, calculated the area of each ring, and then calculated seedling density in each ring per m². For each of the six *P. officinalis* trees, I did a simple linear regression of seedling density vs. distance from trunk.

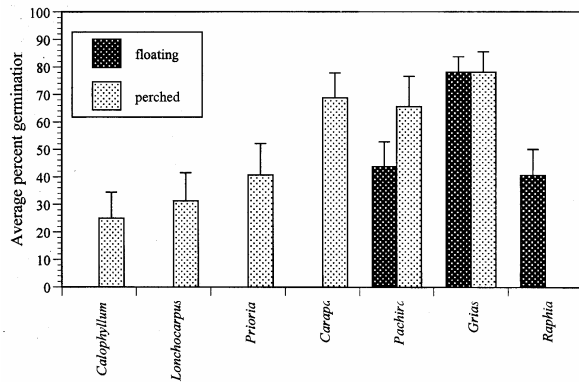


Fig. 2. Average percent germination for swamp tree species in standing water or perched. Error bars are standard error.

Results

Seed germination

The results for seed germination show distinct differences in germination in submerged versus perched conditions (Fig. 2). Only *Grias cauliflora* and *Pachira aquatica* were able to germinate in both conditions. *Carapa guianensis*, *Calophyllum brasiliense*, *Prioria copaifera* and *Lonchocarpus costaricensis* germinated when perched but did not germinate in standing water, whereas *Raphia taedigera* seeds germinated in standing water but did not germinate when perched. Table 2 illustrates the relationships for germination within species.

Table 2. Trends in germination percentages for seven species of swamp trees in perched and wet conditions. Probabilities are from Student's T-tests.

Species	Trend	Probability
<i>Calophyllum brasiliense</i>	Perched > Wet	P = 0.019
<i>Lonchocarpus</i>	Perched > Wet	P = 0.006
<i>Prioria</i>	Perched > Wet	P = 0.003
<i>Carapa</i>	Perched > Wet	P < 0.0001
<i>Pachira</i>	No difference	P = 0.098
<i>Grias</i>	No difference	P = 0.837
<i>Raphia</i>	Wet > Perched	P < 0.0001

In the laboratory experiments with *Pterocarpus officinalis* seeds from Puerto Rico, seeds were able to germinate in both standing water (43% ± 24%) and perched (58% ± 23%). The difference in germination percentages at 90 days was not significant (F=2.30, df=1, P=0.14).

Seedling submersion

All seedlings for all species survived the 0 day (control) and 7 day submersion treatments. Most species also survived the 21 day submersion well. However, for the 42 day treatment, obvious differences arose between species (Exact test, 10 species, 2 outcomes, P<0.0001). Seven species had very high survivorship of the 42 day treatment while three species had poor or no survivorship (*C. guianensis*, *Calophyllum* and *L. costaricensis*; Fig. 3a). *R. mangle*, only tested with 42 days submersion, showed 50% (4 of 8) survivorship.

To test whether there was a Species x Treatment effect for the first three treatments (0, 7, and 21 days submersion), I excluded the 42 days treatment from analysis and performed an ANOVA on percent growth (Fig. 3b) and percent leaf change (Fig. 3c). There were highly significant species and treatment effects for both percent

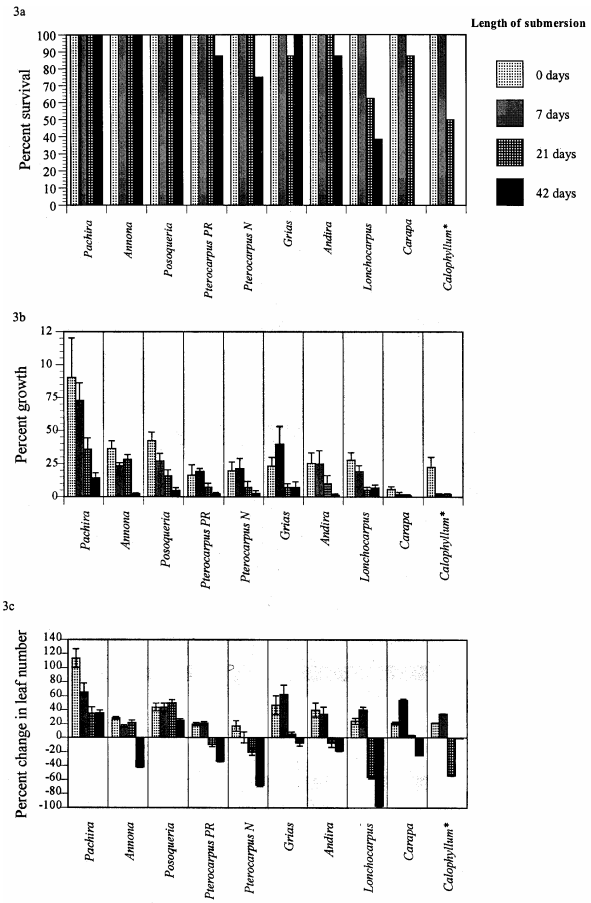


Fig. 3. (a-c) Survival, growth, and change in leaf numbers for seedlings submerged for up to 42 days. All measurements from day 56 of experiment. **Calophyllum brasiliense* was only replicated four times in each treatment due to a limited number of seedlings.

growth in height (%H) and percent leaf change (%L). There was not a significant Species x Treatment effect for percent growth or percent leaf change (Table 3).

Table 3. ANOVA performed on percent changes (day 56 vs. day 0) in height and leaf number of all species for 0, 7, and 21 day submersion.

Variable	Effect	SS	df	MS	F	P
% Height	Submersion Period	1.47	2	0.74	12.81	< 0.0001
	Species	6.12	9	0.68	11.85	< 0.0001
	Species x Submersion	1.11	18	0.61	1.00	0.38
% Leaves	Submersion Period	7.96	2	3.92	25.01	< 0.0001
	Species	10.77	9	1.20	7.52	< 0.0001
	Species x Submersion	5.73	18	0.32	2.00	0.11

The obvious Species x Treatment effect for survivorship of 42 days submersion (Fig. 3a), was further borne out in lack of growth (Fig. 3b) and leaf loss (Fig. 3c) for those species killed by the treatment. To analyze variance among species that survived the 42 day treatment, I excluded the species that did not survive well (*C. brasiliense*, *C. guianensis*, and *L. costaricensis*) and calculated an ANOVA for the remaining six species (including both *Pterocarpus officinalis* groups) for percent growth and leaf loss for the 42 day treatment. Although all these species survived well (minimum 75% survival for 42 days submersion), there were significant differences in the percent growth among species ($F = 3.22$, $df = 6$, $P = 0.01$) and per-

Table 4. ANOVA for survivorship of *Pterocarpus officinalis* seedlings in field experiments on effect of water (standing water vs. perched) and light (shade vs. sun) levels on survivorship.

Variable	Effect	SS	df	MS	F	P
Percent survivorship at 4 months	Water	0.29	1	0.74	1.44	0.25
	Light	0.13	1	0.68	0.64	0.44
	Water x Light	0.01	1	0.61	0.07	0.80
Percent survivorship at 12 months	Water	0.20	1	0.20	0.43	0.43
	Light	0.20	1	0.20	0.43	0.43
	Water x Light	0.96	1	0.96	3.12	0.10

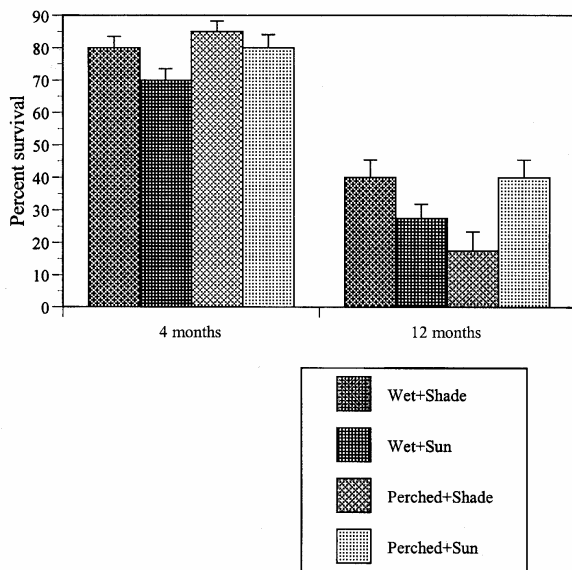


Fig. 4. Percent survival of *Pterocarpus officinalis* seedlings transplanted into different conditions in swamp.

cent change in leaf number ($F = 8.56$, $df = 6$, $P = 0.000002$). Most species had a general pattern of decreased percent growth (Fig. 3b) as submersion length increased. However, it was not typically a stepwise relationship (except *P. latifolia*, Fig. 3b), but percent growth in the 42 day submersion was always distinctly less than for 0 and 7 days. Leaf number decreased in the longer submersion treatments for most species, but *P. aquatica* and *P. latifolia* showed increases in number of leaves for all treatments (Fig. 3c). For the species with little leaf loss, their leaves retained their pre-treatment color. *Pachira aquatica*, *P. officinalis* and *P. latifolia* all had firm, dark green leaves after 42 days submersion.

In the natural analog to submersion experiments using *P. officinalis* in the field, I found no significant differences in survival among conditions at 4 months or 12 months after transplant (Table 4, Fig. 4).

Microtopographic studies

Seedling density was negatively correlated with distance from the trunk for all six *P. officinalis* trees observed. All relationships were highly significant ($0.654 < r^2 < 0.867$, $P < 0.003$ for each of the six regression slopes). Densities of as high as 10 seedlings m^{-2} were observed near the trunks whereas off the buttresses the densities were close to 0 (Fig. 5). On a total of 15 adult *P. officinalis* tree buttresses censused, I observed 11 adult or subadult trees or palms of other species: 3 *C. guianensis*, 4 *G. cauliflora*, 2 *Euterpe* sp. and 2 *Xanthoxylum* sp.

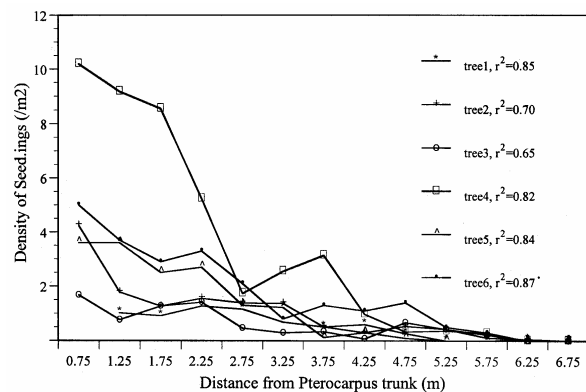


Fig. 5. Seedling density vs. distance from adult *Pterocarpus officinalis*.

Discussion

Flood tolerance

Although the species in the experiments are common and successful swamp trees, several had difficulties with germination in water or submersion of seedlings, two conditions that face swamp species (Table 5). The species that showed difficulties must overcome or escape flooding by some other mechanism to be so successful in swamp forests.

In the submersion experiments, the length of submersion affected growth. The change in percent height with treatment was a result of decreased or zero growth during the submersion, and growth during the recovery period.

Retention of leaves during the submersion by many species provided them with full photosynthetic capabilities upon emergence. In the flooded forests of the Amazon, leaves of seedlings retained had full functional capacity when inundation subsided after several months (Fernandes-Correa & Furch 1992). For seedlings growing in a dark understory of a swamp, flood tolerance of leaves is highly advantageous because regenerating leaves from seed reserves would be energetically costly.

The 42 day maximum duration of submersion of seedlings was likely very appropriate for produc-

ing mortality in even highly flood tolerant species, evidenced by the death of some *R. mangle* seedlings submerged for 42 days. *R. mangle*, the red mangrove, is widely known for its submersion tolerance but was negatively affected by the flooding period. Although principally found in saltwater, *R. mangle* exhibits better growth at lower salinities (Imbert *et al.* 2000) and does well in freshwater swamps in the absence of competition (Vandermeer, pers. comm.). It is present along banks far up into Caño Negro, near Bluefields, Nicaragua, where the river is low-salinity brackish during the dry season and tannic freshwater during the wet season.

The submersion experiments tested the ability of seedlings to survive complete submersion for extended periods. In nature, many seedlings have only their roots and part of their stems covered, thus those species whose seedlings grow tall enough to place their leaves above flood waters may feel the stress of flooding in a different way than my experiments addressed. Root submersion is likely much less difficult for seedlings (Bazzaz & Peterson 1984). The *P. officinalis* seedlings in the "wet treatments" of the field experiment endured root submersion for 12 months in addition to periodic complete submersion, and only suffered mortality similar to that of seedlings on dry ground.

Table 5. Performance of swamp tree species in seed germination and seedling submersion experiments and expected mechanisms for overcoming flooding.

Species	Fruiting period	Dormancy potential	Seed Size (Reserves)	Germinate	Establish	Tolerance	Escape
<i>Raphia taedigera</i>	YR	Long	Medium	W	W*	Sd, Ph	
<i>Pachira aquatica</i>	YR	None	Large	W,P	W,P	Ph	B
<i>Grias cauliflora</i>	WS	None	Medium	W,P	W,P	Ph	D
<i>Pterocarpus officinalis</i>	WS	Some	Medium	W,P	W,P	Ph	
<i>A. inermis</i>	MW	None	Medium	–	W,P	Ph	D
<i>Annona glabra</i>	YR	Some	Small	–	W,P	Ph	D
<i>Posoqueria latifolia</i>	YR	None	Small	–	W,P	Ph	D
<i>Prioria copaifera</i>	EW	Long	Large	P	P*		D,B
<i>Lonchocarpus costaricensis</i>	MW	Short	Small	P	P		D
<i>Carapa guianensis</i>	EW	Long	Large	P	P		D,B
<i>Calophyllum brasiliense</i>	EW	Short	Medium	P	P		D

EW=early in wet season, MW= middle of wet season, WS=throughout wet season, YR=year round, W=in water, P=perched, Sd=seed dormancy, Ph=physiological, B=bolting, D=dispersal. * = inferred from field observations or personal communications. Dormancy potential is a subjective analysis combining seed size and durability of seed (hardness of seed coat, etc.). Seed size is categorized from calculated or measured volumes with large as > 15 ml volume, medium as 5-15 ml volume, and small as < 5 ml volume.

For the submersion experiments, most seeds came from parent trees living in swamps, but the *A. inermis*, *C. brasiliense* and *P. latifolia* seedlings came from parent trees growing in non-inundated soils. Of these three, only *C. brasiliense* was greatly affected by submersion. Keeley (1979) found that *Nyssa sylvatica* seedlings from upland parents fared much more poorly than those from swamps in submersion experiments. Along with the Puerto Rican *C. brasiliense* seedlings not faring well in submersion trials, swamp-collected seeds of this species failed to germinate in standing water. In either test, *C. brasiliense* does not appear to be highly flood tolerant.

Microtopography: Pterocarpus officinalis
buttresses

Adult *P. officinalis* trees provide essential sites for seed germination and seedling establishment above the flood waters of the swamps. In the seedling distribution studies, I had hoped to include adult trees of other species in the study, but they were nearly always growing together with an equal or larger *P. officinalis* tree, suggesting that they had established on the buttresses of that tree and are now crowding it. This was especially true for *C. guianensis* and *C. brasiliense*, which did not show flood tolerance in the two tests I performed. In Nicaragua, *Xanthoxylum* sp. and *Euterpe* sp. are not typically found in swamps but were observed growing there on the buttresses of *P. officinalis*.

Pentaclethra maculosa is a swamp species with no flood tolerance as a seed (Urquhart, unpublished data), and thus, likely needs perches to germinate and establish in swamps. Hartshorn (1983) reports that in swamps, *Pentaclethra* trees have a fairly open base "which may indicate that seedling establishment occurred on a nurse log that has long since disappeared."

Flood tolerant, buttressed trees can be the building blocks for multi-species swamp assemblages. As demonstrated by these studies, many of the best known swamp species lack flood tolerance and may rely upon perched sites for germination and establishment. These species cannot colonize heavily inundated swamps until buttressed species like *P. officinalis* and *Mora* have produced "islands" among the flood waters. *Pterocarpus officinalis* is often considered to be a nuisance species in swamps because of its lack of commercial value,

but its role in swamp ecology may be of vital importance.

Mechanisms of flood tolerance and
flood escape

The flood tolerant species can utilize many characteristics for survival of flooding: (1) seed dormancy through the flooding period, e.g. *Parkia auriculata* (Coutinho & Struffaldi 1971), and (2) physiological tolerance of flooding (Fernandes-Correa & Furch 1992), or (3) seed, bulb, or corm reserves for regeneration of flood-damaged tissues. Seed dormancy must be accompanied by bolting when exposed substrate is encountered or by tolerance of submersion by seedlings. *Parkia auriculata* couples seed dormancy with submersion tolerance to succeed in the Igapó and Várzea forests of the Amazon (Coutinho & Struffaldi 1971). Of the species I studied, *P. aquatica*, *G. cauliflora*, *A. inermis*, *A. glabra*, *P. officinalis*, *R. taedigera*, and *P. latifolia* showed tolerance of flooding, through capacity to germinate in standing water, ability to survive long periods of submersion, or both.

However, for species that do not possess such capabilities, flood-escape mechanisms provide routes for successful germination and establishment in swamps. A diversity of possible mechanisms by which less tolerant species can overcome flooding have been elucidated in other studies: (1) bolting during dry season to place leaves above flood waters, e.g. *Acmena smithii* (Melick 1990), (2) seed production and germination during periods of low water (often in conjunction with mechanism 1), (3) colonization of microsites above flood waters, e.g. *Fraxinus caroliniana*, *Nyssa sylvatica* var. *biflora* and *Sabal palmetto* (Titus 1990). The necessity of bolting to place leaves above flood waters is frequently proposed as the reason for the relatively large seeds of many swamp species (McHargue & Hartshorn 1983a).

Although *C. brasiliense*, *C. guianensis* and *L. costaricensis* are widely distributed swamp specialists, they all were unable to germinate in standing water or survive long periods of seedling submersion. The adult trees are obviously tolerant of root flooding, but the species are not flood tolerant at critical stages early in life. *Prioria copaifera* is similar to *C. brasiliense*, *C. guianensis* and *L. costaricensis* in not being able to germinate in standing water and probably does not fare well when seedlings are submerged, because it is not found in

extremely wet swamps in Panama (T. A. Kursar, personal communication). All of these species produce fruit at the beginning of or in the middle of the usual wet season and thus must cope with a substantial period of standing water. Their diverse natural histories hold clues about the mechanisms each utilizes to escape flooding.

Calophyllum brasiliense is bat-dispersed. Typically, bats remove a fruit from the parent tree and fly to a feeding roost to process the seed, then dropping the seed (Janzen *et al.* 1976). Thus, *C. brasiliense* seeds are likely to fall under other swamp trees. *Pterocarpus officinalis* and *Mora oleifera* Ducke (Caesalpinaceae) both have extensive buttress networks that can provide elevated sites for germination and establishment and *C. brasiliense* may be dependent upon such species for reproduction.

Carapa guianensis is dispersed by mammals and by water. Seeds will float until they perch or rot (Fanshawe 1947). Scatter-hoarding by rodents is probably the most common dispersal route for *C. guianensis*, since the rodents would bury the seeds in exposed soil (McHargue & Hartshorn 1983b). With its large seed reserves, *C. guianensis* is able to bolt to place its leaves above flooding. Bolting becomes advantageous if waters rise further in the late wet season to flood the germination sites of *C. guianensis*.

Prioria copaifera appears to be primarily water dispersed, although Croat (1978) suggests that mammals may play a role in dispersal. White-faced capuchins (*Cebus capuchinus*) often consume the seeds but are very destructive and are not likely dispersers (Hladik & Hladik 1969). Agoutis (*Dasyprocta agouti*) are similarly destructive (Urquhart, unpublished data). Standley (1928) thought that peccaries were dispersers of *P. copaifera* but feeding tests showed white-lipped and collared to be indifferent to the seeds (Urquhart, unpublished data). Other mammals (Tapirs, Coatis) ignored the bitter, chalky seeds. When collecting seeds, I found a significantly disproportionate number of the perched seeds had germinated when compared to floating seeds (Urquhart 1997). *Prioria copaifera* is a durable seed that may float dormant until it reaches a suitable site for germination.

Lonchocarpus costaricensis, the other species with difficulties establishing in a flooding swamp, is different yet. It is not a common species in the

interior of the swamps of Nicaragua, being found only along the riverbanks. The seeds are wind and water dispersed, and are probably swept into mats of debris collecting along the riverbanks. Atop the debris, the seeds could germinate and establish, eventually rooting themselves down to the swamp soil. Table 5 summarizes the results of the experiments and expected mechanisms for flood tolerance and flood escape.

There is a limit to flood-escape mechanisms. *Camposperma panamensis* Standl. (Anacardiaceae) is a hardwood of Central American swamps that lacks flood tolerance (Phillips 1995), thus likely employs flood-escape mechanisms for survival in swamps. Phillips (1995) found that *Camposperma panamensis* can be greatly affected by changes in swamp water level. In Nicaragua, paleoecological analysis showed that the extremely flood tolerant *Raphia taedigera* replaced *Camposperma panamensis* as the dominant species in the swamps about 2500 B.P. Sea level rise over the past millenia is probably responsible for the disappearance of the once dominant *C. panamensis* from Nicaraguan swamps. Changes in water levels, precipitation patterns, or other major environmental change will greatly endanger these species.

The flood intolerance of species like *C. brasiliense*, *C. guianensis* and *P. copaifera* has great practical importance. Each of these is very important as a timber species and is found in monodominant forests. The encouragement of these species in forest management of swamps will require understanding the mechanisms they utilize for flood-escape. The elevated sites provided by the buttresses of *P. officinalis* are also important in terms of species management in swamps. Without these microsites for germination and establishment, many of the desired swamp species may not be able to colonize.

The research presented here demonstrates that not all species commonly found in swamp forests are flood tolerant. Many of the species utilize flood-escape mechanisms to cope with flooding. The diverse natural histories of tropical trees provide a diversity of flood-tolerance and flood-escape mechanisms. Although it is not possible to determine whether these mechanisms are adaptations or simply fortuitous characters that allow the species to make their ways into swamps, flood-tolerance and flood-escape mechanisms are vital to the species of swamp forests.

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