Germination characteristics and establishment of trees from central Amazonian flood plains

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Abstract: In central Amazonian flood plains, seedlings after few months are submerged for up to 210 days every year. Among 31 analysed tree species, those from high levels in the flooding gradient germinated earlier and had longer leaves and taller seedlings than those from low levels. Species with hypogeal germination dominated with 59.1%, compared to 40.9% with epigeal germination. 80% of the chosen species from nutrient-poor igapó had hypogeal germination with big, fleshy cotyledons, in contrast to 30% in nutrient-rich várzea. Species with high seed mass growing at high elevations in the flooding gradient in igapó had higher percent germination, and significantly bigger leaf length and seedling height. The four species with seed mass >25 g had hypogeal germination, and the 13 species with seed mass below 1 g all had epigeal germination with foliaceous cotyledons. All species depended on emersion of the soil for germination.

Resumen: En planicies de inundación de la Amazonía Central, las plántulas después de unos pocos meses están sumergidas por hasta 210 días cada año. Entre las 31 especies arbóreas analizadas, aquéllas propias de los niveles altos en el gradiente de inundación germinaron más tempranamente y tuvieron hojas más largas y plántulas más altas que las propias de niveles bajos. Las especies con germinación hipógea fueron dominantes con 59.1%, en comparación con 40.9% de las que tienen germinación epígea. 80% de las especies seleccionadas del igapó, que es pobre en nutrientes, tuvieron germinación hipógea con cotiledones grandes y carnosos, lo cual contrasta con 30% en la várzea, que es rica en nutrientes. Las especies cuyas semillas tienen una masa grande y que crecen en las mayores elevaciones del gradiente de inundación en el igapó tuvieron un mayor porcentaje de germinación, así como longitud foliar y altura de sus plántulas significativamente mayores. Las cuatro especies con masa de las semilla >25 g tuvieron germinación hipógea, y todas las 13 especies con masa de la semilla por debajo de 1 g presentaron germinación epígea con cotiledones foliáceos. La germinación de todas las especies fue dependiente de la emersión del suelo.

Resumo: Nas planícies alagadas da Amazónia Central, o nascedio, depois de alguns meses, é submergido todos os anos até mais de 210 dias. Entre as 31 espécies arbóreas analisadas verificou-se que aquelas dos níveis mais elevados do gradiente de cheia germinavam mais cedo e dispõem de folhas maiores e plantas mais altas do que as dos níveis mais baixos. As espécies com germinação hipógina eram dominantes com uma representação de 59.1% em comparação com os 40.9% com germinação epígena. Verificou-se que 80% das espécies escolhidas nos solos pobres em nutrientes do igapó apresentam uma germinação hipógina com cotilédones grandes e tenras, em contraste com o valor de 30% para a várzea rica em nutrientes. As espécies com sementes com massa alta, vegetando nas zonas de mais alta elevação do gradiente de alagamento no igapó, apresentam as maiores percentagens de germinação e comprimentos de folhas e altura das plantas significativamente maiores. As quatro espécies com uma semente com massa > 25 g apresentam germinação hipógina, enquanto que as 13 espécies com semente de menor massa, abaixo de 1 g, apresentam germinação epígena com cotilédones foliáceos. Todas as espécies dependem da emersão do solo para a germinação.

Key words: Flood plain forest, flooding gradient, seed germination, seedling establishment, submergence, survival strategies.

Introduction

Several hundred tree species grow in central Amazonian flood plains which are subject to extended periods of flooding. With a flood amplitude exceeding 10 metres, seedlings are completely submerged for up to seven months every year (Junk 1989) and the time for seedling establishment in the non flooded terrestrial period is reduced to a few months or weeks.

Various critical steps have to be managed until the establishment of a tree (Primack 1990). The first step is efficient seed dispersal, which in Amazonian flood plains is mainly anemo-, hydro- and zoochorous (Goulding 1980; Kubitzki & Ziburski 1994; Ziburski 1991). Once a seed has been deposited, it is critical whether the soil is flooded or not. Duration and timing of germination are the next step for efficient establishment: if time to germination is short, the reduced terrestrial period can be efficiently used for growth of the seedling. Timing is important, because if a seed germinates too early, the flood might not have receded and growth of the young seedling can be inhibited by flooding. If it germinates too late, valuable time is lost before the next flood begins (Parolin 2001). The cotyledon expansion mode (epigeal / hypogeal germination) can play key roles for the early establishment (Hladik & Miquel 1990). The food reserves in the cotyledons are available for the seedling only if their longevity is long enough (Burtt 1991). The number of leaves and seedling height achieved before the next aquatic phase can be responsible for its survival with flooding. Characteristics like time to germination and initial morphology of the seedlings are closely related to the strategies of establishment of a species at a specific site (Ng 1978). In the present paper, the role of seed size and germination type, the occurrence in the flooding gradient, and the environment in which the species typically grow - nutrient-rich whitewater flood plains called várzea, or nutrient-poor blackwater flood plains called igapó - are analysed for 31 typical tree species from central Amazonian flood plain forests.

Material and methods

Seed collection

Seeds were collected in the flood plains of the Amazon river and Rio Negro near Manaus, Brazil. During the rising period of the rivers in 1994 to 1996 (March-July), up to 50 mature fruits and seeds of each species were collected floating in the water or directly from the trees, chosing at least 5 trees per species. Fruits and seeds were placed in plastic bags, transported to the laboratory and put into small basins with river water for storage until the begin of the experiments and to break the potential dormancy (Ziburski 1991).

All chosen species are common in central Amazonian flood plains (Prance 1979; Worbes *et al.* 1992) and represent a range of different growth strategies, with species from várzea or from igapó, from different positions in the flooding gradient, evergreen and deciduous species, as well as pioneer and non-pioneer species (sensu Swaine & Whitmore 1988) (Table 1). The classification of 'species from várzea' and 'species from igapó' is based on where the seeds were collected, and that the species does not occur in the other ecosystem. Species growing mainly between 18 and 25 m asl were classified as 'low' (subjected to long periods of inundation) on the gradient (Ayres 1993; Ferreira 1991, 1997; Ferreira & Stohlgren 1999; Parolin & Ferreira 1998; Parolin 2000a). The germination type was classified according to seedling morphology in the experiments: the epigeal type has the cotyledons above the ground level and develops seedlings with upright, leafy cotyledons; the hypogeal type has fleshy cotyledons at or under the soil (Hladik & Miquel 1990; Primack 1990).

Table 1. Species selected for this study, with flood plain system where the species occur and the seeds were collected.

	Species	Family	Flood-plain system	Level in flooding gradient	Successional stage	Leaf phenology	Germination type
1	*Acmanthera latifolia*	Malpighiaceae	igapó	-	NP	-	-
2	*Aldina latifolia*	Caesalpiniaceae	igapó	H	NP	E?	H
3	*Annona hypoglauca*	Annonaceae	várzea	L	NP	-	-
4	*Campsiandra comosa*	Caesalpiniaceae	igapó	L	NP	E	H
5	*Cecropia latiloba*	Cecropiaceae	várzea	L	P	E	E
6	*Crateva benthami*	Capparidaceae	várzea	L	NP	D	E
7	*Crudia amazonica*	Caesalpiniaceae	várzea	L	NP	D	H
8	*Elaeoluma glabrescens*	Sapotaceae	igapó	-	NP	-	-
9	*Erisma calcaratum*	Vochysiaceae	igapó	-	NP	-	-
10	*Eschweilera tenuifolia*	Lecythidaceae	igapó	L	NP	E	-
11	*Ficus insipida*	Moraceae	várzea	H	NP	-	E
12	*Hevea spruceana*	Euphorbiaceae	igapó	L	NP	E	H
13	*Macrolobium acaciifolium*	Caesalpiniaceae	igapó	H	NP	E	H
14	*Mora paraensis*	Caesalpiniaceae	igapó	H	NP	D	H
15	*Nectandra amazonum*	Lauraceae	várzea	L	NP	E	H
16	*Ormosia excelsa*	Papilionaceae	igapó	L	NP	D	H
17	*Parkia discolor*	Mimosaceae	igapó	L	NP	D	E
18	*Pentaclethra macroloba*	Mimosaceae	igapó	H	NP	-	H
19	*Piranhea trifoliata*	Euphorbiaceae	várzea	L	NP	D	-
20	*Poecilanthe amazonica*	Papilionaceae	igapó	H	NP	-	-
21	*Pouteria glomerata*	Sapotaceae	várzea	L	NP	E	-
22	*Psidium acutangulum*	Myrtaceae	várzea	L	NP	D	E
23	*Salix humboldtiana*	Salicaceae	várzea	L	P	E	E
24	*Senna reticulata*	Caesalpiniaceae	várzea	H	P	E	E
25	*Simaba guianensis*	Simaroubaceae	igapó	L	NP	E	-
26	*Swartzia laevicarpa*	Papilionaceae	igapó	H	NP	E	H
27	*Swartzia polyphylla*	Papilionaceae	igapó	H	NP	E?	H
28	*Symmeria paniculata*	Polygonaceae	igapó	L	NP	E	E
29	*Tabebuia barbata*	Bignoniaceae	várzea	L	NP	D	H
30	*Vatairea guianensis*	Papilionaceae	igapó	H	NP	E?	H
31	*Vitex cymosa*	Verbenaceae	várzea	L	NP	D	E

(várzea = nutrient rich whitewater flood plains, igapó = nutrient poor blackwater flood plains), elevation in the flooding gradient (H high: 25-28 m asl, L low: 18-25 m asl, - no data), successional stage (P pioneer/NP non-pioneer; sensu Swaine & Whitmore 1988), leaf phenology (E evergreen/D deciduous/- no data), and germination type (H hypogeal/E epigeal, - no data).

Seed germination and seedling development

Seed germination and seedling development were analysed in the Amazon Research Institute (INPA) in Manaus / Brazil at an experiment site which was sunny in the morning and in the afternoon, but shady between 11.00 and 14.00 h (Fig. 1).

(a) Germination tests: Germination (species did/did not germinate) and duration to germina-

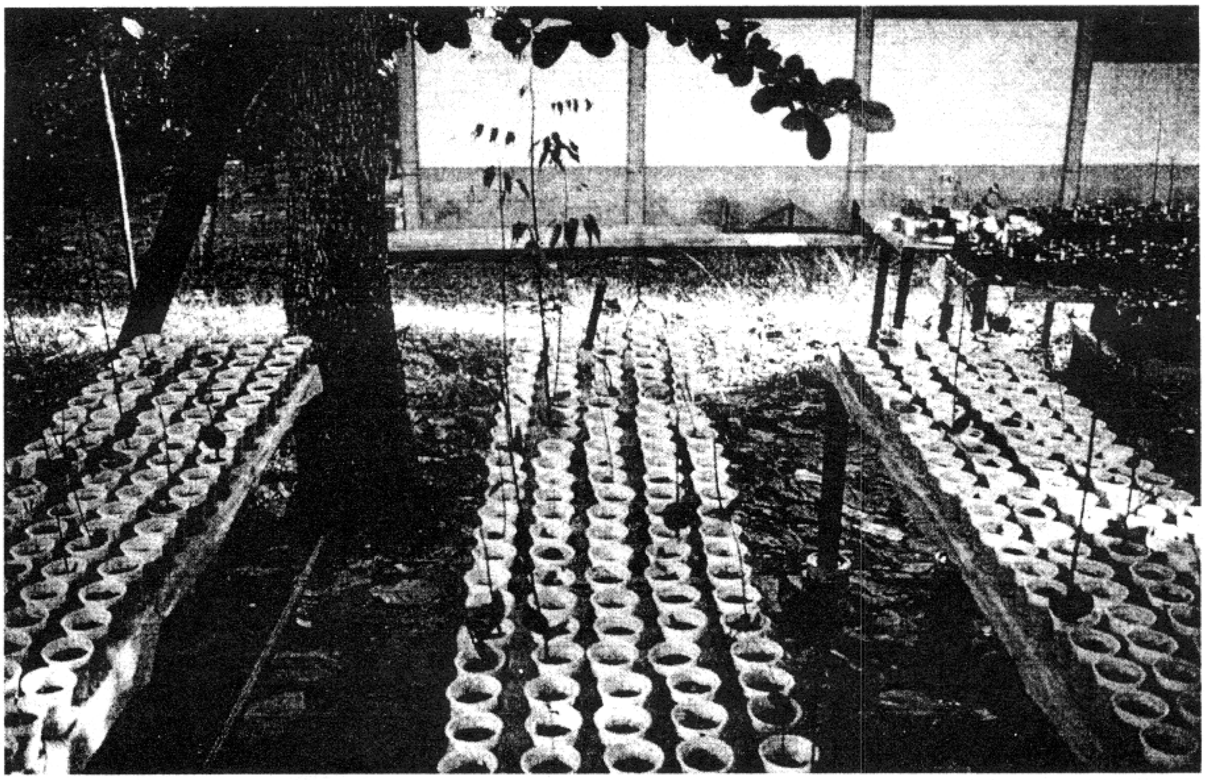

Fig. 1. Experiment site at the Amazon Research Institute (INPA) / Manaus.

tion were determined qualitatively in 31 species placed into plastic cups (300 ml) on mixed soil from várzea and igapó. 25 seeds per species were tested, each seed was placed in one plastic cup. Germination defined as shoot emergence was checked daily. Percent germination was calculated by the amount of seeds germinated after 7 weeks in relation to total initial seed number (in percent).

(b) Submerged germination: 10-30 seeds were subjected to the same conditions as in the germination experiment (*a*), but the cups were filled with Amazon river water submerging seeds and soil.

(c) Seedling development: The expansion time and longevity of cotyledons, duration of leaf expansion, leaf number, leaf length and seedling heights were measured at 3 days interval for the seedlings from the above experiment (a). The results 12 weeks after experiment start are presented.

(d) Epigeal and hypogeal germination: The experiment (c) was split in species with epigeal and hypogeal germination, and was used to compare germination and seedling growth.

(e) Flooding gradient: The experiment (c) was also split in species which typically grow at high (10 species) and low (18 species) elevations in the flooding gradient, and was used to compare germination and seedling growth.

(f) Species from várzea and igapó: The data set (c) was split in species from nutrient-rich várzea (13 species) and from nutrient-poor igapó (18 species), and germination and seedling growth were compared.

(g) Seed weight in relation to seedling growth: In a former study, seed weight of 58 species was analysed (Parolin 2000a). These data are put in relation with seed germination and seedling growth.

Results

(a) Germination test: In 31 analysed species, percent germination after 7 weeks varied between 5 and 100% in the seeds in well watered soil, with an average of 50%. The limitation to 7 weeks (49 days) was chosen because this was the time by which all species had a percent germination of at least 5%. Time to germination was between 3 and 49 days (Table 2). The fastest germination with the given conditions occurred in *Salix humboldtiana* (3 days), the slowest in *Annona hypoglauca* and *Hevea spruceana* (49 days).

Table 2. Seed germination (shoot emergence) of 31 tree species from central Amazonian flood plains after 7 weeks: percent germination, duration until germination and cotyledon opening, and cotyledon longevity.

Species	Germination [%]	Days until germination (mean ± S.D.)	Days until cotyledon opening (mean ± S.D.)	Cotyledon longevity (days mean ± S.D.)
Acmanthera latifolia	15	39 ± 11	40 ± 8	43 ± 3
Aldina latifolia	55	18 ± 8	24 ± 10	-
Annona hypoglauca	5	49 ± 0	-	-
Campsiandra comosa	20	24 ± 2	35 ± 7	-
Cecropia latiloba	50	14 ± 5	0.3 ± 0.2	25 ± 2
Crateva benthami	90	7 ± 1	10 ± 3	17 ± 4
Crudia amazonica	30	16 ± 5	32 ± 12	-
Elaeoluma glabrescens	80	17 ± 3	26 ± 4	44 ± 4
Erisma calcaratum	20	9 ± 2	17 ± 9	47 ± 23
Eschweilera tenuifolia	50	20 ± 1	-	-
Ficus insipida	20	28 ± 4	24 ± 7	-
Hevea spruceana	5	49 ± 0	49 ± 0	-
Macrolobium acaciifolium	90	9 ± 3	10 ± 3	25 ± 6
Mora paraensis	100	8 ± 6	15 ± 4	47 ± 5
Nectandra amazonum	55	11 ± 4	26 ± 5	56 ± 0
Ormosia excelsa	55	6 ± 2	21 ± 8	50 ± 6
Parkia discolor	45	8 ± 7	7 ± 3	16 ± 4
Pentaclethra macroloba	45	9 ± 5	15 ± 7	-
Piranhea trifoliata	45	15 ± 4	22 ± 10	45 ± 10
Poecilanthe amazonica	75	17 ± 6	29 ± 9	-
Pouteria glomerata	100	16 ± 5	24 ± 7	47 ± 11
Psidium acutangulum	50	19 ± 4	27 ± 5	46 ± 5
Salix humboldtiana	5	3 ± 0	-	-
Senna reticulata	85	6 ± 3	1 ± 1	26 ± 6
Simaba guianensis	10	40 ± 23	-	30 ± 0
Swartzia laevicarpa	5	36 ± 0	36 ± 0	-
Swartzia polyphylla	90	8 ± 3	14 ± 7	-
Symmeria paniculata	75	7 ± 1	17 ± 3	-
Tabebuia barbata	30	11 ± 6	10 ± 3	44 ± 6
Vatairea guianensis	100	5 ± 2	11 ± 7	41 ± 8
Vitex cymosa	60	13 ± 3	1 ± 0	18 ± 4
Average	50	17	20	35

- no data

(b) Submerged germination: There was no germination observed for the submerged seeds in all 31 chosen species. Seeds remained after the experiment were put into plastic vessels with water for storage. They remained viable for at least three months if the water was changed frequently,

while seeds which were kept in the air dried or decomposed within few weeks.

(c) Seedling development: On the average, it took 20 (± 12) days to expand the cotyledons in all the 31 species, with a minimum of 0.3 days (*Cecropia latiloba*) and a maximum of 49 days (*Hevea spruceana*) (Table 2). Mean cotyledon longevity, the duration until their fall or deterioration, was 35 (± 13) days after complete cotyledon expansion. Minimum cotyledon longevity was 16 days (*Parkia discolor*) and maximum was 56 days (*Nectandra amazonum*) (Table 2). The first leaf was expanded after an average of 13 ± 5 days after shoot germination, with a minimum of 2.8 days in *Tabebuia barbata* and a maximum of 29 days in *Crudia amazonica* (Table 3). At a seedling age of one

Table 3. Time from shoot germination to expansion of the first leaf, and mean number of expanded leaves, leaf length and seedling height at a seedling age of one month.

Species	Time to first leaf [days after shoot germination]	sd	Mean number of expanded leaves	sd	Mean leaf length [cm]	sd	Mean seedling height after one month [cm]	sd
Acmanthera latifolia	-	-	1.4	1.0	1.8	1.3	2.7	0.8
Aldina latifolia	-	-	2.8	1.3	7.1	3.4	62.2	26.1
Annona hypoglauca	-	-	2.0	0.0	2.6	0.0	-	-
Campsiandra comosa	-	-	1.5	0.7	6.8	0.4	23.0	2.8
Cecropia latiloba	8.3	3.0	-	-	-	-	-	-
Crateva benthami	4.8	0.9	2.2	0.4	5.4	0.5	8.7	1.0
Crudia amazonica	29.0	0.0	3.6	2.2	7.4	2.1	33.8	7.2
Elaeoluma glabrescens	-	-	2.0	0.0	7.5	1.2	9.8	1.7
Erisma calcaratum	-	-	4.0	2.8	10.0	6.9	22.1	8.6
Eschweilera tenuifolia	-	-	-	-	-	-	-	-
Ficus insipida	-	-	-	-	-	-	0.9	0.7
Hevea spruceana	-	-	-	-	-	-	16.5	2.0
Macrolobium acaciifolium	23.3	4.6	4.4	1.1	14.3	1.6	43.5	8.4
Mora paraensis	-	-	2.7	1.2	12.3	4.2	73.5	24.4
Nectandra amazonum	8.2	3.2	6.2	2.2	6.3	3.0	23.8	5.0
Ormosia excelsa	-	-	2.9	2.8	8.0	3.3	17.2	2.3
Parkia discolor	-	-	2.6	2.3	3.2	2.2	10.8	3.7
Pentaclethra macroloba	-	-	2.9	1.7	13.2	5.9	24.8	5.8
Piranhea trifoliata	-	-	2.7	0.5	3.2	0.8	7.5	1.7
Poecilanthe amazonica	-	-	2.0	1.4	7.5	5.6	13.8	9.3
Pouteria glomerata	-	-	1.8	0.9	6.2	3.8	12.5	4.6
Psidium acutangulum	-	-	5.9	1.1	2.9	0.6	6.1	1.3
Salix humboldtiana	-	-	-	-	-	-	-	-
Senna reticulata	6.6	1.2	3.5	0.9	1.9	0.4	5.4	0.8
Simaba guianensis	-	-	-	-	-	-	0.8	0.2
Swartzia laevicarpa	-	-	-	-	-	-	-	-
Swartzia polyphylla	-	-	3.4	1.8	8.2	3.7	92.2	34.0
Symmeria paniculata	27.7	4.1	-	-	-	-	-	-
Tabebuia barbata	2.8	1.7	3.7	0.6	6.6	1.2	9.0	2.1
Vatairea guianensis	-	-	8.6	2.6	13.3	3.3	99.7	30.1
Vitex cymosa	6.0	2.7	3.3	1.3	2.5	0.5	5.1	0.6

- no data

month, mean number of leaves was 3.3 ± 1.7, varying from 1.4 (*Acmanthera latifolia*) to 8.6 (*Vatairea guianensis*). The average leaf length was 6.9 ± 3.8 cm, varying between 1.8 cm (*Acmanthera latifolia*) and 14.3 cm (*Macrolobium acaciifolium*). Mean height of the seedlings was 25 ± 17.9 cm at an age of one month. Seedling height varied between 0.9 cm (*Ficus insipida*) and 99.7 (*Vatairea guianensis*) (Table 3).

(d) Epigeal and hypogeal germination: The duration to shoot emergence (germination) and to cotyledon expansion were longer in species with hypogeal germination (Fig. 2). These species had higher cotyledon longevity, higher number of expanded leaves, higher leaf length and greater seedling height than species with epigeal germination (Table 4).

(e) Flooding gradient: Species from high elevations in the flooding gradient had a higher percent germination, shorter time to shoot emergence and cotyledon opening, and a significantly higher leaf length and seedling height than species from low elevations (Table 4).

(f) Species from várzea and igapó: Differences between species from nutrient-rich várzea and species from nutrient-poor igapó were found in the time to first leaf expansion, mean leaf length and seedling height: they all were higher in species from igapó (Table 4).

(g) Seed weight in relation to seedling growth: Large seeds had short germination time and greater seedling height (Table 5) than species with small seeds.

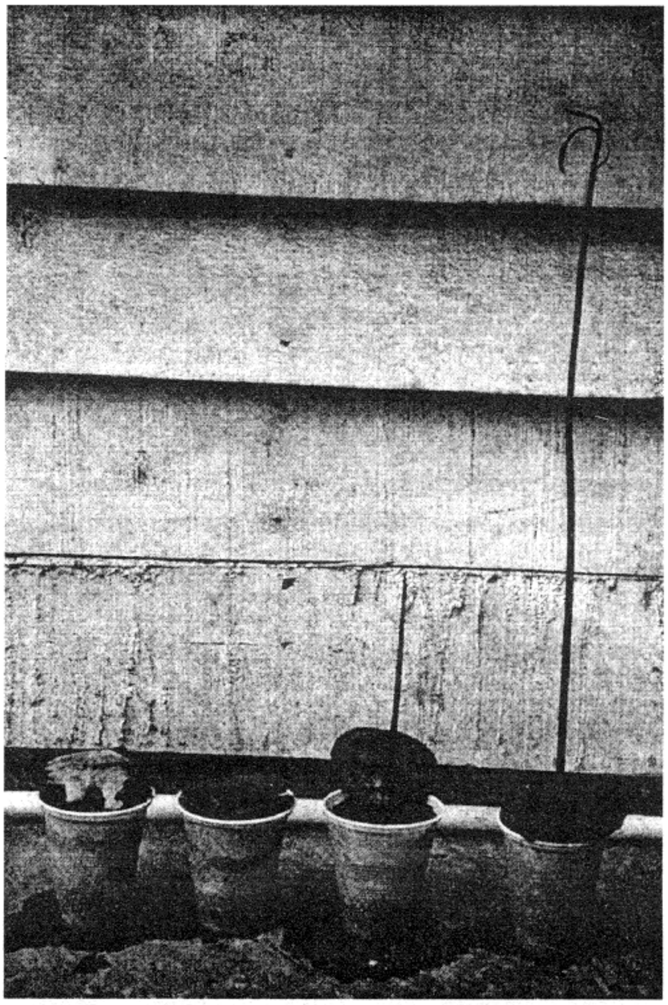

Fig. 2. Germinating *Mora paraensis*, an example for hypogeal germination.

Table 4. Comparison of species with epigeal or hypogeal germination, species growing at high or low elevations in the flooding gradient, and species from nutrient-rich várzea and nutrient-poor igapó.

Parameters	Epigeal germination	Hypogeal germination	High levels	Low levels	Species from Várzea	Species from Igapó
Germination (%)	53.3	52.3	66.5	43.3	48 ± 31	52 ± 33
Days until germination (mean)	11.8	16.2	14.5	18.2	16 ± 12	18 ± 14
Germination (%): seeds flooded	0.0	0.0	0.0	0.0	0 ± 0	0 ± 0
Days until cotyledon opening (mean)	10.9	22.9	17.8	20.1	16 ± 12	23 ± 12
Cotyledon longevity (days)	24.5	41.4	34.8	34.1	33 ± 16	37 ± 14
Days to first expanded leaf (mean)	13.1	11.7	16.1	11.1	7 ± 3	26 ± 3
Mean number of expanded leaves	3.5	3.9	3.8	3.2	4 ± 2	3 ± 2
Mean leaf length (cm)	3.2	9.4	9.7	5.1	5 ± 2	9 ± 4
Mean height after 1 month (cm)	6.2	43.3	46.2	13.4	11 ± 10	34 ± 32

Table 5. Seed weight and seedling growth of the 31 species chosen for this study, with flood plain system, level in the flood gradient (H high, L low), and germination type (E epigeal, H hypogeal).

Species	Seed weight	Seed weight category	Days to germination	Days to leaf emergence	Cotyledon longevity	Seedling height	Flood-plain system	Level in flooding gradient	Germination type
Acmanthera latifolia			long		long	low	igapó		
Aldina latifolia	69.4	heavy	short			high	igapó	H	H
Annona hypoglauca	0.4	light	long				várzea	L	
Campsiandra comosa	6.1	light	short			low	igapó	L	H
Cecropia latiloba	0.002	light	short	short	short		várzea	L	E
Crateva benthami	0.2	light	short	short	short	low	várzea	L	E
Crudia amazonica	6.4	light	short	long		low	várzea	L	H
Elaeoluma glabrescens			short		long	low	igapó		
Erisma calcaratum			short		long	low	igapó		
Eschweilera tenuifolia	3.1	light	short				igapó	L	
Ficus insipida			long			low	várzea	H	E
Hevea spruceana	4.1	light	long			low	igapó	L	H
Macrolobium acaciifolium	1.4	light	short	long	short	low	igapó	H	H
Mora paraensis	38.5	heavy	short		long	high	igapó	H	H
Nectandra amazonum	2.0	light	short	short	long	low	várzea	L	H
Ormosia excelsa	0.7	light	short		long	low	igapó	L	H
Parkia discolor	0.3	light	short		short	low	igapó	L	E
Pentaclethra macroloba			short			low	igapó	H	H
Piranhea trifoliata	0.05	light	short		long	low	várzea	L	
Poecilanthe amazonica	0.8	light	short			low	igapó	H	
Pouteria glomerata	0.3	light	short		long	low	várzea	L	
Psidium acutangulum	0.1	light	short		long	low	várzea	L	E
Salix humboldtiana	0.002	light	short				várzea	L	E
Senna reticulata	0.01	light	short	short	short	low	várzea	H	E
Simaba guianensis			long		long	low	igapó	L	
Swartzia laevicarpa			long				igapó	H	H
Swartzia polyphylla	30.2	heavy	short			high	igapó	H	H
Symmeria paniculata	0.02	light	short	long			igapó	L	E
Tabebuia barbata	0.3	light	short	short	long	low	várzea	L	H
Vatairea guianensis	26.5	heavy	short		long	high	igapó	H	H
Vitex cymosa	0.2	heavy	short	short	short	low	várzea	L	E

Separation of categories always at 50 % of highest recorded value, i.e. seed weight light = 0-24 g, heavy ≥ 25 g; days to germination short = 0-25, long ≥ 26; days to leaf emergence short = 0-15, long ≥ 16; cotyledon longevity short = 0-28 days, long ≥ 29 days; seedling height low = 0-50 cm, high ≥ 51 cm.

Discussion

Among the 31 studied species, there was not a main trend to ensure survival and establishment in the flood plains, but diverse strategies can be found. There are species which have short and long periods of germination.

Role of germination duration

Among the six species with long duration to germination (more than 25 days), there are species from várzea and igapó, from high and low levels in the flooding gradient, and with epigeal and hypogeal germination (Table 5). The common trait among these species was that they did not have big seeds, and they reached only low seedling height. It is possible that these species are highly flood tolerant, and total submergence does not affect the seedlings to a considerable extent. Unfortunately, no data is available on the flood tolerance of these species and their seedlings. Among the 25 species with less than 25 days to germination all combinations (várzea/igapó, high/low levels in flooding gradient, epigeal/hypogeal germination) can be found as well (Table 5).

Role of the germination type

The hypogeal species dominate compared to epigeal germination. This is very similar to the findings of Moreira & Moreira (1996), where 59.5% of the species of the family of Leguminosae from Amazonian flood plains had hypogeal germination. This germination type seems to be more efficient in the flood plains. The investment of time was higher in the 13 species with hypogeal germination. It took longer to germinate and to expand the cotyledons than in species with epigeal germination. The advantages may be related to the achieved seedling size: in the same period of time, the seedlings with hypogeal germination were almost eight times as high as the seedlings with epigeal germination, and the leaves were three times longer. This might help the respective species to withstand long periods of submergence.

On the other hand, a considerable number (9) of species had epigeal germination. Species growing outside the forest or in disturbed areas, especially fast-growing pioneers, typically have epigeal germination with the rapid formation of foliaceous cotyledons which are responsible for the first photosynthetic activities and rapid growth because it only has limited energetic reserves (Hladik & Miquel 1990; Primack 1990). In this study, the three pioneer species had epigeal germination, as well as other species which typically establish at forest margins (e.g. *Crateva benthami*, *Symmeria paniculata*). Fast germination and cotyledon opening probably helps to efficiently use the little time between the floods.

Seeds found in seed banks in the soil generally have epigeal germination with foliaceous cotyledons (Hladik & Miquel 1990), but the species from Amazonian flood plains do not have seed-banks in the water or in the sediments (Junk, pers. comm.).

Effect of position in the flood gradient

The vast majority of tree species from Amazonian flood plains can establish, and perhaps persist, in a variety of habitats and can be considered habitat generalists (Ferreira & Stohlgren 1999). Most species are adapted to a wide range of habitats and flood durations and there is not a strict restriction to one level in the flood gradient. Still, most species have their optimum linked to their flood tolerance, and they are more successful in one habitat rather than another. The selected species which normally grow only at high levels, germinated earlier (Table 4) and had longer leaves and taller seedlings than the species from low levels. This might be explained by a lower flood tolerance of the species of the higher levels, and to their need to maintain a part of the plant over the water surface to be able to survive. *Senna reticulata*, for example, does not tolerate complete submergence, but can survive if at least few leaves are kept above the water surface (Parolin 1998). This species grows so rapidly that it is not covered by flooding: plant height after 11 months was the same (4.59 m) as bambus species can achieve (Leeuwen *et al.* 1998). Again, unfortunately, little is known about the flood tolerance of the species analysed in the present study. In other flood plain species, *Erythrina glauca* (Papilionaceae) and *Hevea brasiliensis* (Euphorbiaceae), the relation between seedling height before flooding and survival to the flooded period was positive (Leeuwen *et al.* 1998). For *Ocotea cymbarum* (Lauraceae) and *Genipa americana* (Rubiaceae) Leeuwen *et al.* (1998) found no relation between size and survival – may be these species have higher tolerance to submergence. Species growing at low elevations have to be able to tolerate long periods of inundation, both as seedlings and as adult plants. Therefore, they need other strategies, e.g. morphological and anatomical adaptations to submergence (Schlüter & Furch 1992; Schlüter *et al.* 1993; Waldhoff *et al.* 1998). Survival cannot be ensured by fast growth (Parolin 2000 a), although plant size (leaf area, plant height and mass) may be an important determinant of competitive ability (Gerry & Wilson 1995).

Várzea and Igapó

Since nutrient resources are distinct in várzea and igapó, it might be expected that seedlings are subjected to different selective pressures for estab-

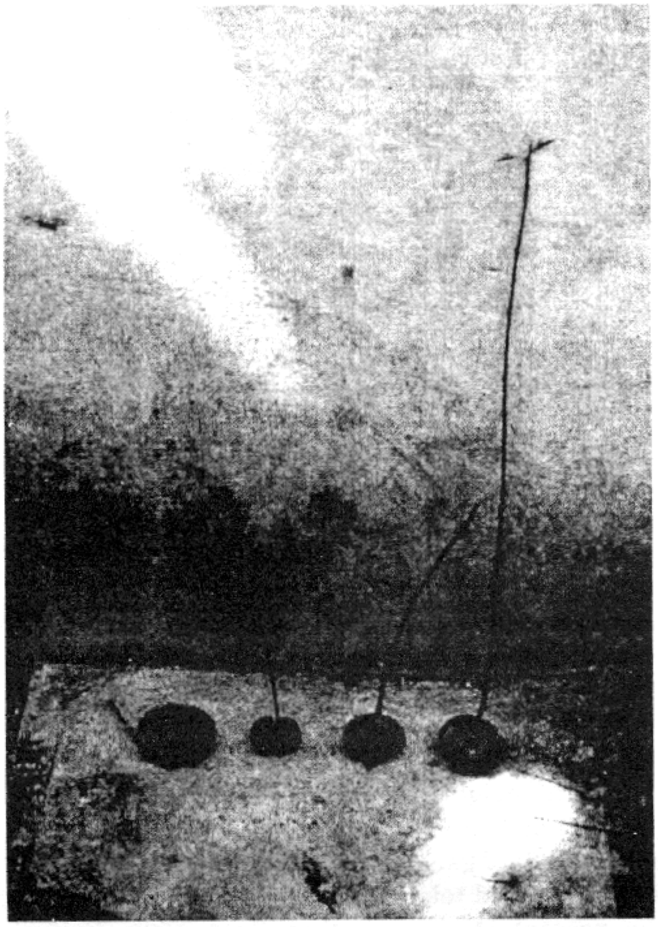

Fig. 3. Germination of *Aldina latifolia* seeds on a concrete floor (Amazon Research Institute INPA) / Manaus): the seeds germinated and grew to a height of > 1.20 m without soil and water.

lishment. In fact, 80% of the chosen species from nutrient-poor igapó had hypogeal germination with big, fleshy cotyledons, in contrast to nutrient-rich várzea where it were 30% (Table 6). The high percentage of species with hypogeal germination in igapó could be linked to the lack of nutrients: the function of the cotyledons is to supply the establishing plant with nutrients or to represent the first photosynthetic organ before the first leaves are expanded. In várzea, the environment provides sufficient nutrients to the establishing seedling, whereas in igapó the resources have to be supplied by the mother plant. This is underlined also by the fact that in igapó 78% of the chosen species had long cotyledon longevity, compared to 56% in várzea (Table 6). Mean leaf length and seedling height were higher in the first weeks in species from igapó than in those from várzea. It is possible that the conditions for germination and growth at the experimental site were not favourable for all species. This is clearly the case for the pioneer species, *Cecropia latiloba*, *Salix humboldtiana* and *Senna reticulata* which under natural conditions, in full light, reach heights up to one metre in the same time as only some centimeters were achieved in the experiment (Parolin 1997, 1998; Oliveira & Piedade in press). The differences of leaf length and seedling height between species from igapó and várzea might also be linked to the large cotyledons which enable fast growth in the first period of establishment. The importance of seed reserves and cotyledons are shown by seeds of *Aldina latifolia* which were forgotten on a concrete floor: they germinated and grew to a height of more than 1.20 m without soil and water (Fig. 3). In the absence of any mineral nutrients other than those in the seed seedlings of heavier seeded-species tend to survive longer than seedlings from lighter-seeded species (Jurado & Westoby 1992).

Among the 23% of igapó seedlings (4 species) which reached big height in the experiment (Table 6), all have big seeds with weights above 26 g (Parolin 2000 a) and which are able to grow fast also without any light or nutrient supply from the environment.

Table 6. Comparison of the species from várzea (13 species) and igapó (18 species). Values are in percentage.

		Várzea	Igapó
Successional stage	pioneers	23	0
	non-pioneers	77	100
Phenology	evergreen	45	77
	deciduous	55	23
Germination type	epigeal	70	17
	hypogeal	30	83
Level in flood gradient	high	39	80
	low	61	20
Seed weight	high	0	33
	low	100	67
Duration to germination	short	85	78
	long	15	22
Cotyledon longevity	short	44	22
	long	56	78
Seedling height	high	0	27
	low	100	73

The role of seed size

The significant differences between seed mass of species from várzea (average 1.16 g, Parolin 2000 a) and igapó (average 7.08 g) can add some explanation to understand the differences between early seedling growth in the two ecosystems. Seed size may influence emergence time, and indirectly affect competitive ability of a seedling (Gerry & Wilson 1995). It has a strong influence on the probability of germination, seedling size, growth rate, seedling establishment and survivorship (Murali 1997). The number of days for germination was positively related to seed size in Indian species: smaller seeds germinated faster than larger seeds (Murali 1997). Small-seeded temperate species in Japan had a longer duration of leaf emergence, shorter leaf longevity, and rapid leaf turnover, compared to big-seeded species (Seiwa & Kikuzawa 1996). In várzea and igapó, the big-seeded species always had short duration to germination, whereas the small-seeded species germinated fast or slow (Table 5). Whether early germination in big-seeded species is simply a result of higher seed mass, or an adaptation e.g. against the attack of predators and pathogens (Seiwa 1998), is not clear here.

Leaf longevity and turnover were not tested in this study, but small-seeded species like the pioneers *Senna reticulata*, *Cecropia latiloba*, and *Salix humboldtiana* have short leaf longevity and rapid leaf turnover compared to other species (Parolin 1997; Oliveira & Piedade in press).

The higher seed mass of species from high elevations in the flooding gradient in igapó (average 27.8 g, compared to means of 1.1 g at low elevations, and 0.2 g and 1.3 g in high and low positions in várzea, respectively; Parolin 2000 a), is reflected by a higher percent germination, and significantly bigger leaf length and seedling height of the species from high elevations in igapó than from low levels or from both levels in várzea (Table 7). 100% of the species from high elevations in igapó had hypogeal germination, compared to 50% in the other species. It is probable that this germination strategy is the most effective at the conditions given at these sites, in order to allow fast growth and enable the seedlings to 'escape' from flooding.

Different seedling types may correspond to the same seed size class, involving different physiological adaptations to germination. The four species with seed mass >25 g had hypogeal germination, and the 13 species with seed mass below 1 g all had epigeal germination with foliaceous cotyledons (with the exception of *Tabebuia barbata*, Table 5). This correlates with the study by Moreira & Moreira (1996), where species of the family of Leguminosae from Amazonian flood plains with small seeds had exclusively epigeal, species with big seeds exclusively hypogeal germination. Epigeal germination may be advantageous for small seeds without storage organs to utilize light energy as rapidly as possible, through the foliaceous cotyledons (Hladik & Miquel 1990). In the

Table 7. Comparison of the species from igapó and várzea at high and low levels in the flooding gradient.

Parameters	Igapó		Várzea	
	High	Low	High	Low
Germination (%)	70 ± 33	37 ± 26	53 ± 46	47 ± 30
Days until germination	14 ± 10	22 ± 17	17 ± 15	16 ± 12
Days until cotyledon opening	19 ± 9	26 ± 16	12 ± 10	17 ± 12
Cotyledon longevity (days)	38 ± 11	33 ± 24	26 ± 12	34 ± 14
Days to first expanded leaf	23 ± 8	28 ± 12	9 ± 4	7 ± 3
Number of expanded leaves	4 ± 2	2 ± 1	4 ± 2	3 ± 2
Leaf length (cm)	11 ± 3	6 ± 2	2 ± 1	5 ± 2
Height after 1 month (cm)	59 ± 33	14 ± 8	6 ± 2	13 ± 10
Seed weight (g)	27.8± 25	2.4 ± 2	0.01 ± 0	0.9 ± 0.4
Number of species	8	7	2	11
Percentage with hypogeal germination	100	60	0	38

species with hypogeal germination energy reserves are carried by the seeds themselves, and germination below a closed canopy is favoured.

Conclusions

All 31 species chosen for this study depended on emersion of the soil for germination. Their life cycles are closely linked to the flooding periodicity ('flood pulse', Junk *et al.* 1989), and the time for germination and establishment is reduced. Each seedling type represents a functional adaptation to forest regeneration, with special relationships to seed size, seed dispersal, and plant establishment (Hladik & Miquel 1990). The efficient germination and early growth are especially important in this ecosystem since not all species tolerate submergence in the first weeks or months after establishment and the few favourable months have to be efficiently used. Despite these difficulties, a high species number and many different growth traits and life strategies were found among the chosen species, and each species may have a particular type of seedling which is best adapted to a particular set of conditions, such as light, moisture, temperature, duration of flooding, and predators. With this study, we hope to contribute to the understanding of the ecology of trees in Amazonian flood plains, including species of commercial interest. Many species of the flood plains are of high commercial value, for timber production as well as non-timber products (Parolin 2000b), but basic knowledge about their establishment and growth requirements is still very small (Ferraz 1991). By simple observations of seed size and seedling morphology – added by detailed experiments – it is possible to predict the preferred habitat and light requirements of seedlings, and this information can be used by forestry nurseries in developing general methods for propagating different seedling types (Primack 1990).

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