

# Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains

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## Abstract

In Amazonian floodplains, plants are subjected to prolonged periodical flooding with a water column of up to 10 m. Seedlings are submerged, except if they establish in the upper parts of the inundation gradient and grow so fast to be able to maintain some leaves above the water surface. The hypothesis of this study is that there are mainly two strategies for seedling establishment in Amazonian floodplains: tolerance of prolonged submergence vs. escape from submergence. Measurements of height increase in relation to floodplain system and nutrient availability, height in the inundation gradient, and seed mass of 31 common species indicated that the two hypothesized strategies enable efficient seedling establishment on different levels in the flooding gradient. Where submergence is unavoidable, on the lower sites in the flooding gradient, seedlings had significantly lower shoot extension than on the higher sites. Large and small seeds produced seedlings with high shoot elongation, enhancing the chances of non-submergence for the seedlings at high elevations. This pattern was evident also within the family of Fabaceae, taking into account the effect of relatedness among species. In igapó high seed mass compensated the lack of nutrients of the environment. In nutrient-rich várzea, nutrients are supplied by the environment and seeds are smaller, but they may produce seedlings which are just as tall. This emphasizes the strong selective pressure for tall seedlings on high elevations in the flooding gradient. It is assumed that the zonation observed in Amazonian floodplains is directly linked to the flooding tolerance and establishment strategy of the seedlings, and less to the tolerance of the adult trees. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Floodplain forest; Flooding gradient; Growth; Seed germination

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## 1. Introduction

Seedling establishment is a critical step in tree life (e.g. Foster and Janson, 1985; Kelly and Purvis, 1993), and plant colonization of flood-prone habitats is little understood to date (Ernst, 1990; Scarano, 1998), particularly in Amazonian

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floodplains where prolonged periodical floodings with a water column of up to 10 m at average occur every year (Junk, 1989). The growth and flooding tolerance of the seedlings are reflected in a zonation of tree species along the inundation gradient, with tolerant species growing on lower levels, and less tolerant species growing on higher levels (Ferreira, 1997, 2000). In this ecosystem, seedlings are always subjected to submergence, except if they establish in the upper parts of the inundation gradient and grow so fast to be able to maintain some leaves above the water surface. Although in flood-prone habitats seedling establishment may be confined to years with anomalous water levels, the role of two consecutive years of low water levels for tree establishment seems to be less important in Amazonian floodplains. The age structure of the forests indicates that all age classes are represented (Worbes et al., 1993; Worbes, 1989), and individuals of one species do not result from one or few single establishment events. The periodicity and predictability of the flood pulse (Junk et al., 1989) allowed the evolution of adaptations and strategies to cope with the adverse growth conditions which predominate for several months every year (Colwell, 1974). The hypothesis of this study is that there are mainly two survival strategies for seedling establishment in Amazonian floodplains: tolerance of prolonged submergence vs. escape from submergence. The species which do not tolerate submergence and 'escape' from it need adaptations which are not necessarily required by the species from low levels that tolerate prolonged submergence which they cannot escape from. Seedlings with the 'escape-strategy' have to grow fast on the higher levels in the flooding gradient, in order to maintain at least part of the plant above the water surface. When elongation results in a protrusion of leaves above the water surface the plants survive, because they can restore a free diffusion pathway between the air and the root system which is of vital importance for some species (Laan and Blom, 1990). Rapid juvenile growth enables the plants to extend their foliage as high as possible before the normal flood level returns, but this requires high nutrient supply, which the species in nutrient-rich white water

floodplains (várzea) find in the sediment-rich environment (Furch, 1997, 2000). In nutrient-poor black water floodplains (igapó), nutrients for early seedling growth have to be supplied by the mother plant, as demonstrated by higher seed mass of species from igapó (Parolin, 2000a). It is expected that at high levels in the flooding gradient, seedlings grow taller than at low levels, with high seed mass in igapó and high or low seed mass in várzea. Species from low levels in the flooding gradient have lower seed mass in both igapó and várzea (Parolin, 2000a). They are not expected to have a specially fast height increase since plants cannot escape from submergence. The probability of a seedling to be able to grow over the water level is low and only highly flood tolerant species can survive there. They need other strategies than fast growth to tolerate several weeks to months of submergence, e.g. physiological and morphological adaptations (Siebel et al., 1998). Obviously these two contrasting patterns of plant adaptation to flooding, submergence tolerance vs. escape from submergence, are not necessarily mutually exclusive, and highly tolerant, fast-growing species may be expected as well as not tolerant, slow-growing species. Still, the differentiation between cryptocotylar seedlings which use their seed reserves to quickly extend their shoots and escape from the flooding hazard, and slow-growing phanerocotylar seedlings which withstand long-term submersion is not new (Coops and Van der Velde, 1995; Scarano, 1998).

In the present study, measurements of height increase in relation to floodplain system, height in the inundation gradient, and seed mass are used to test the hypothesis that two contrasting strategies, tolerance of prolonged submergence vs. escape from submergence, enable survival of seedlings in Amazonian floodplains. Since species do not necessarily represent independent data points there is a need to take into account the effect of relatedness among species (Kelly and Purvis, 1993) which was done here focussing comparisons at high elevations in the flooding gradient on species of the Fabales, the most important families with fruits dispersed by water in Amazonian floodplains (Kubitzki, 1985).

## 2. Methods

Seeds of 31 species (Table 1) were collected in the floodplains of the Amazon (Solimões) river and Rio Negro near Manaus, Brazil.

Mature seeds of each species were collected floating in the water or directly from the trees. Since not all species produced mature fruits at the same time, the seeds were placed in plastic bags, transported to the laboratory and put into small basins with river water for conservation until the beginning of the experiments.

At a maximum, they were kept for 2 weeks floating in the water. All chosen species are common in Central Amazonian floodplains (Prance, 1979; Worbes et al., 1992), with species from várzea or from igapó, and from different positions in the flooding gradient. The classification of 'species from várzea' and 'species from igapó' is based on the sites where the seeds were collected, which does not mean that the species are not present in the other ecosystem: they can be restricted to one of the ecosystems, or occur in both, or even occur in terra firme (Ayres, 1993; Kubitzki, 1989a,b; Rosales et al., 1999; Worbes, 1983; Worbes et al., 1992). The elevation in the flooding gradient was defined according to Ayres (1993), Parolin and Ferreira (1998), Ferreira and Stohlgren (1999), and Parolin (2000a): species typically growing between 25 and 28 m above sea level (asl) were classified as 'high' on the flooding gradient (subjected to short periods of inundation), corresponding to the 'high-level tree community' which is exposed to less than 140 days of flooding per year (Junk, 1989). Species growing mainly between 18 and 25 m asl were classified as 'low' (subjected to long periods of inundation) on the gradient and belong to the low- to mid-level tree community, which is exposed to up to 270 days of flooding per year (Junk, 1989). This classification was not only based on literature, but was also confirmed in the field. In the study sites near Manaus, mainly on the Ilha de Marchantaria (várzea) and in the Rio Tarumã Mirim (igapó), the chosen species were confined to the environment to which they were classified.

Seedling development was analysed in the Amazon Research Institute (INPA) in Manaus/Brazil.

In a total of 680 plastic cups (300 ml), 25 seeds per species were planted, each in a separate cup which was well watered daily. The soil used in the cups was 50% várzea sediment + 50% igapó sand collected on the Ilha de Marchantaria (várzea) and in the Rio Tarumã Mirim (igapó). According to Furch (1997), at specifically these sites the average pH of both soils is 3.5–4, their contents of available nutrients are: N 110/132, P 49/41, K 426/139, Mg 1395/45, Ca 8900/79 ( $\text{kg ha}^{-1}$  in várzea/igapó, respectively). At the experimental site, an open site with maximum photon flux densities were between 1.500 and 2.300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , maximum air humidity 85% and maximum air temperature was 36 °C. Seedling height was monitored at weekly intervals. The same plant age was considered from the time of germination up to the time of treatment to avoid bias due to late germinating species. Seed mass data were taken from Parolin (2000a). Three species did not germinate under the given conditions (*Amanoua oblongifolia*, *Ilex inundata* and *Symme-ria paniculata*) and were excluded a priori from the calculations. The data were subjected to analysis of variance to test for significance of differences between height growth in species from high and low positions (1 degree of freedom).

## 3. Results

### 3.1. Seedling height growth

Height growth was significantly distinct in species from high and low levels ( $F$ -ratio = 119.080,  $P = 0.0001$ ). All the seedlings which germinated after 1–5 weeks and had continuous height growth were considered in the calculations. After 11 weeks, the seedlings from high elevations were almost three times taller than the seedlings from species which commonly occur at low elevations (Fig. 1). Species from várzea and igapó had similar height growth at low elevations. In species from high elevations, a distinct growth pattern was measured in species from várzea and igapó, with a constant height increase in species from várzea and a fast height increase in the fourth to seventh week and little increase thereafter in spe-

Table 1  
Species chosen for this study, with indication whether they normally occur in nutrient-rich várzea or in nutrient-poor igapó, and on high or low elevations in the flooding gradient

	Species	Family	Common name	Fruits DM (g)	sd	Seeds DM (g)	sd	n	Height after 11 weeks (cm)	sd
Igapó, high elevations	<i>Aldina latifolia</i> Spruce ex Benth.	Caesalpinaceae	Macucu	75.9	23.8	69.40	27.3	10	62.2	3.9
	<i>Macrobium acaiaifolium</i> Benth.	Caesalpinaceae	Arapari da folha miúda	3.9	1.2	1.40	1.0	5	50.0	5.2
	<i>Mora paraensis</i> Ducke	Caesalpinaceae	Pracuúba	95.6	30.6	38.50	11.8	10	73.5	5.8
	<i>Pentaclethra macroleoba</i> (Willd.) Kuntze	Mimosaceae	Pracaxi	-		5.40	1.1	10	25.0	5.4
	<i>Poecilanthæ amazonica</i> Benth.	Fabaceae	Anambi	4.5	1.5	0.80	0.2	9	18.0	3.0
	<i>Swartzia polyphylla</i> DC	Fabaceae	Araba	38.4	18.2	30.20	7.1	10	92.2	6.3
	<i>Swartzia argentea</i> Benth.	Fabaceae		8.4	2.1	3.60	0.8	10	21.6	8.5
	<i>Vatairea guianensis</i> Aubl.	Fabaceae	Fava	30.7	9.5	26.50	6.6	10	99.7	5.2
	<i>Erisma calcaratum</i> (Link) Warm.	Vochysiaceae		2.6	1.1	0.40	0.0	5	17.3	3.7
	<i>Amanoa oblongifolia</i> Aubl.	Euphorbiaceae	Uxi	0.2	0.0	0.043	0.0	10		
	<i>Hevea spruceana</i> Muell. Arg.	Euphorbiaceae	Seringa	36.0	6.9	4.10	0.9	10	32.0	5.0
	<i>Campsandra comosa</i> Benth.	Caesalpinaceae	Acapurana	40.3	9.0	6.10	0.8	10	22.3	2.3
	<i>Ormosia excelsa</i> Benth.	Caesalpinaceae	Tento amarelo	1.8	0.2	0.70	0.1	5	19.5	2.0
	<i>Parkia discolor</i> Benth.	Mimosaceae	Arara tucupi	11.2	1.1	0.28	0.0	10	11.3	3.3
	<i>Acananthera latifolia</i> Benth.	Malpighiaceae		0.1	0.0	0.012	0.0	5	4.5	0.4
	<i>Symmeria paniculata</i> Benth.	Polygonaceae	Carauacu	0.1	0.0	0.017	0.0	5		
Igapó, low elevations	<i>Alibertia edulis</i> (L. Rich.) A. Rich.	Rubiaceae	Apurui	1.0	0.1	0.014	0.0	10.0	32.7	3.8

Table 1 (Continued)

Species	Family	Common name	Fruits DM (g)	sd	Seeds DM (g)	sd	n	Height after 11 weeks (cm)	sd
<i>Elaeoloma glabrescens</i> (Martius & Eichler)	Sapotaceae		1.4	0.8	0.8	0.2	10	10.3	1.5
Aubréville									
<i>Pouteria elegans</i>	Sapotaceae	Abiu	1.8	0.9	1.30	0.5	10	13.8	4.2
Eyma									
<i>Senna reticulata</i> (Willd.) Irwin & Barneby	Caesalpinaceae	Matapasto	0.6	0.0	0.013	0.0	10	63.5	19.9
<i>Platymiscium ulei</i> Harms	Fabaceae	Macacaúba	0.2	0.0	0.19	0.0	6	43.0	3.8
<i>Ilex inundata</i> Poepp. ex Reiss	Aquifoliaceae	Turima	0.1	0.0	0.013	0.0	4		
<i>Tabebuia barbata</i> (E. Mey.) Sandw. Eichl. in Mart.	Bignoniaceae	Capitari	9.2	1.2	0.26	0.1	10	8.3	3.2
<i>Cratva benthami</i> Miq.	Capparidaceae	Catoré	44.4	11.7	0.21	0.0	10	10.3	1.5
<i>Cecropia latiloba</i> Miq.	Cecropiaceae	Imbaúba branca	25.8	1.9	0.002	0.0	10	6.8	2.4
<i>Piranhea trifoliata</i> Baill.	Euphorbiaceae	Piranheira	0.5	0.1	0.06	0.0	10	8.4	2.2
<i>Nectandra amazonum</i> Nees	Lauraceae	Louro	3.7	0.6	2.03	0.5	10	25.5	1.5
<i>Crudia amazonica</i> Spruce ex Benth.	Caesalpinaceae	Orelha de cachorro	12.6	4.0	6.40	1.6	10	32.7	6.2
<i>Psidium acutangulum</i> DC	Myrtaceae	Araça	4.7	0.8	0.11	0.0	10	9.3	2.0
<i>Pouteria glomerata</i> (Miq.) Radlk.	Sapotaceae	Abiu	8.2	2.0	0.33	0.0	3	14.3	2.6
<i>Vitex cymosa</i> Benth.	Verbenaceae	Taruma	0.4	0.1	0.21	0.0	10	10.1	6.8

Fruit and seed dry mass (DM) (according to Parolin, 2000a), and height after 11 weeks were measured.

cies from igapó. At 11 weeks, the seedlings had reached similar heights in both várzea and igapó species.

### 3.2. Seedling height in relation to seed mass

Most species from high levels in igapó had high seed mass and tall seedlings (Table 1). Four species are clearly out of the range of the others (*Vatairea guianensis*, *Mora paraensis*, *Swartzia polyphylla* and *Aldina latifolia*). The other five species from igapó which grow at high levels are in the range of the species from low levels in both várzea and igapó. Most species from low levels in várzea have very small seed masses and little height growth, whereas the species which grow at high elevations in várzea, *Senna reticulata* and *Platymiscium ulei*, both reach high seedling heights with small seed size.

### 3.3. Seedling height growth within Fabales

Comparing species within the Fabales, the differences between species from high and low levels in igapó remained almost unchanged (Fig. 2). In species from várzea, those from high levels were a little taller than those from low levels, but the differences were very small. It has to be considered that the sample size in this case was very small (1–2), therefore statistical analyses could not be performed here.

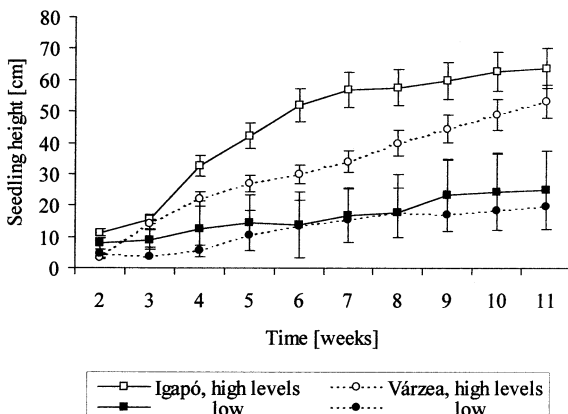


Fig. 1. Height growth of species from high and low levels in igapó and várzea under experimental conditions in the INPA/Manaus, Brazil.

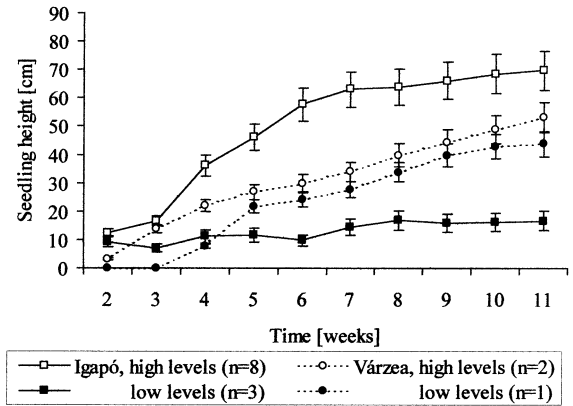


Fig. 2. Height growth of species of the Fabaceae from high and low levels in igapó and várzea under experimental conditions in the INPA/Manaus, Brazil.

### 3.4. Seedling height in relation to seed mass within Fabales

Four species of the Fabales from high levels in igapó were clearly separated from the other species (Fig. 3). Species from igapó with high seed mass had tall seedlings, and also those species with seed mass below 10 g had taller seedlings than species from low levels in igapó with low seed mass. In the species from várzea, very small seed mass was correlated with relatively high seedlings in the two Legume species.

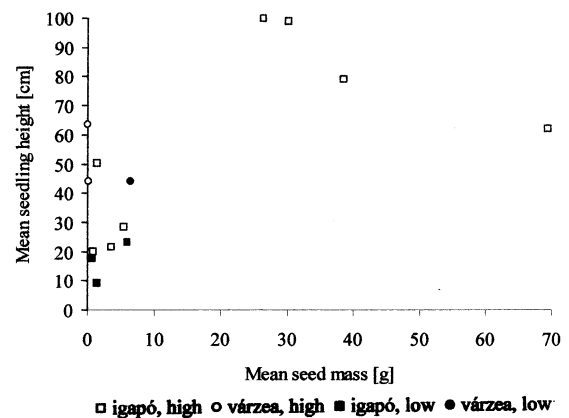


Fig. 3. Relation between seed mass and seedling height at the age of 11 weeks in species of the Leguminosae from high levels in the flooding gradient in igapó □ and in várzea ○, and from low levels in the flooding gradient in igapó ■ and in várzea ●.

#### 4. Discussion

Two main strategies enable efficient seedling establishment in Amazonian floodplains, as indicated by the growth patterns and seed masses of 31 species analysed in this study: tolerance of prolonged submergence, and escape from submergence. Where submergence is unavoidable, on low levels in the flooding gradient, seedlings tended to have significantly lower shoot extensions than on higher sites (Fig. 1). Within the Fabales, average seedling height at 11 weeks was more than four times higher in the species from high levels (Fig. 2), enhancing the chances of non-submergence. The three legume species from várzea achieved heights which were intermediate to those of igapó species from high and low levels (Fig. 2). Perhaps in várzea higher seedlings have advantages at all sites since sedimentation rate is high (Irion et al., 1983) and low seedlings may easily be buried. Overall stability may be higher if the seedlings are taller (Murali, 1997), and nutrients are not a limiting factor in the várzea. In igapó where nutrients are an important limiting factor (Furch, 1997, 2000), establishment strategies must be more focussed on the avoidance of need for nutrients from the environment. Species from low elevations often grow slowly also after the seedling stage, as indicated by lower annual increment rings as compared to trees in várzea (Worbes, 1989; Parolin and Ferreira, 1998). Further analyses of sapling and tree growth are needed here.

##### 4.1. The role of seed mass

Differences in seed mass are thought to reflect the different problems posed for seedling establishment (Harper et al., 1970; Westoby et al., 1990). The data of the present study indicate that seed mass may be directly related to seedling growth in some species, but environmental conditions influence the adaptive seedling growth as well. At high levels in the flooding gradient seedlings grew taller than at low levels, with high seed mass in igapó and low seed mass in várzea. This was especially evident within the Fabales (Fig. 3). Large and small seeds produced seedlings with high shoot elongation. Interestingly, small

seeds from species of high elevations produced taller seedlings than seeds of the same size from species of low elevations (e.g. *Macaranga acaciifolia* vs. *Pouteria elegans* seed mass 1.4 g, height after 11 weeks 50 cm vs. 14 cm, respectively). Seedling growth thus reflects both evolutionary responses to habitat and influences of seed size (Long and Jones, 1996). Seeds of the várzea tend to be smaller than seeds of the igapó (Parolin, 2000a), but they may produce seedlings which are just as tall. This states the selective pressure for higher seedlings on high elevations in the flooding gradient. Seed size was not only higher because many species have spongy pericarps which allow hydrochloric dispersal (Kubitzki, 1985). Large seed size is thought to supply an ample nutrient reserve necessary for seedling establishment (Hewitt, 1998) and helps to survive the loss of photosynthetic tissue better than smaller seeded species. Consequently, large seed size may be favoured in any circumstances in which seedlings are likely to experience nutrient deficits early in development (Armstrong and Westoby, 1993). In fact, the amount of protein, fat and carbohydrates was between 70 and 90% of all analysed seeds, both in species with low and high seed mass (Waldhoff et al., 1996; Waldhoff and Alencar, 2000).

##### 4.2. Establishment and plant zonation

Spatial separation is a matter of degree of specialization (Hook and Scholtens, 1978), and the elevation in the flooding gradient is a surrogate for flood tolerance (Hall and Harcombe, 1998) just as seedling tolerance to flooding is responsible for distributional patterns and colonization (Scarano et al., 1997). Early life-history characteristics of the species relate to their locations in the riparian zonation (Coops and Van der Velde, 1995). It is assumed here that the zonation observed in Amazonian floodplains (Junk, 1989; Ferreira, 1997) is directly linked to the flooding tolerance of the seedlings, and less to the tolerance of the adult trees which hardly ever are completely submerged and during the whole year show high phenological and physiological activity despite prolonged waterlogging (Parolin, 2000b). The tolerance of total submergence may increase

with age: seedlings of species characteristic of low-lying sites in the temperate zone, such as *Alnus glutinosa* and *Populus nigra*, had a higher tolerance in their second or third year than species from higher sites (Siebel and Blom, 1998).

The species from low levels, which have to tolerate submergence, need adaptations to cope with the prolonged period of unfavourable conditions. The capacity to make photosynthesis under water has been postulated for some species (Fernandes-Corrêa and Furch, 1992; Schlüter and Furch, 1992) and can be of fundamental importance for survival. Other species—mostly from várzea—shed their leaves, are dormant during the period of complete flooding and resprout soon after the water recedes (Parolin, 2001a). At high levels in the flooding gradient, the need for such adaptations is smaller and the important strategy is fast height growth as has been shown in the várzea for *Senna reticulata*. This species does not tolerate submergence but grows 4 m in 8 months which enables survival in the highest levels of the flooding gradient where it exclusively occurs (Parolin, 2001b). Some large-seeded species from igapó (seed mass > 30 g, e.g. *Aldina latifolia*, *Mora paraensis* and *Swartzia polyphylla*) have been described as extremely intolerant to submergence (Kubitzki and Ziburski, 1994; Ziburski, 1991). They occur only at high levels, and seedlings grew to a height of 2 m without nutrient, light and water supply as observed occasionally in seeds germinated on a concrete floor under a roof (Parolin, 2001c) demonstrating the capacity for fast height growth, and the independence of these species from external nutrient supply in the first weeks after germination.

Some species which are subjected to regular periods of flooding direct all responses to waterlogging towards gaining oxygen, by shoot elongation and protrusion of the leaves above the water surface (Laan and Blom, 1990). Other species slow down metabolism upon submergence contributing to preservation of starch reserves in the tap-root and, consequently, to the capacity of regrowth on de-submergence. In order to understand species distributions along the flooding gradient, further analyses are needed, e.g. of physiological adaptations. Since seedling size

varies within species and depends on emergence time, microsite variation, genetic variability and on the environmental conditions (Gerry and Wilson, 1995), also studies which consider intraspecific growth differences are needed.

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