Seed mass in Amazonian floodplain forests with contrasting nutrient supplies

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(Accepted 12th December 1999)

ABSTRACT. In the Central Amazonian floodplains, several hundred tree species grow in areas that are periodically flooded by nutrient-rich white-water rivers (várzea) and by nutrient poor black-water rivers (igapó). Seed masses of 31 species from várzea and 27 species from igapó were compared taking into consideration their taxonomic relatedness. Overall average seed mass was higher (mean = 7.08 g) in nutrient-poor igapó than in nutrient-rich várzea (mean = 1.16 g). In igapó, the species growing at high elevations on the flooding gradient had significantly higher seed masses than the species growing at low elevations. In várzea, no difference was found between species growing at high and low elevations. Four large-seeded species from igapó occurring at high elevations on the flooding gradient were responsible for most of the difference in average seed mass between forest types. These data suggest that at low positions in the flooding gradient in igapó, selection pressure on seed size is probably the same as in várzea. At sites with short periods of flooding in igapó forests, on high levels in the flooding gradient, the need for rapid height growth may have selected for species with larger seeds which enable seedlings to be less dependent on soil nutrients.

RESUMO. Na Amazônia Central, centenas de espécies de arvores crescem em áreas inundadas tanto por rios de água branca (vŕzea), ricos em nutrientes, como por rios de agua preta (igapós), pobres em nutrientes. O peso médio das sementes de 31 espécies de várzea e de 27 espécies de igapó foi comparado considerando também relações taxonómicas. A média de peso das sementes foi maior no igapó (média = 7.08 g) do que na várzea (média = 1.16 g). No igapó, as espécies que crescem em níveis altos do gradiente de inundação tiveram os pesos de sementes significativamente maiores do que nos níveis baixos, sujeitos a períodos mais longos de inundação. Na várzea, não houve diferenças entre espécies de níveis altos e baixos. Quatro espécies de igapó, com sementes grandes, típicas de níveis altos no gradiente de inundação, foram responsaveis pelas diferenças da média de peso das sementes. Os dados deste estudo sugerem que no igapó, em posições baixas do gradiente, a pressão seletiva sobre o peso das sementes provavelmente

é semelhante a da várzea. No igapó, em sítios com períodos curtos de inundação, em níveis altos do gradiente, a necessidade de crescimento rapido das plántulas pode ter selecionado sementes maiores que favorecem uma independência maior dos nutrientes do solo.

KEY WORDS: flooding gradient, floodplain forests, igapó, nutrient supply, seedling establishment, seed mass, seed weight, várzea

INTRODUCTION

In Central Amazonia, several hundred tree species occur in two types of floodplains, those flooded periodically by white-water rivers (várzeas) and those by black-water rivers (igapós) (Prance 1979). Climate and hydrological regimes are almost identical in the two systems close to the confluence of the Rio Negro and the Amazon (Solimões) River. The periodicity of flooding and its amplitude of up to 14 m are similar, but different selective pressures seem to operate in the two systems, resulting from the different nutrient statuses. The areas flooded periodically by white-water rivers have a high sediment input and the soils are comparatively nutrient-rich, while the areas flooded by black-water rivers have little sediment input and the soils are very poor (Sioli 1954, Sombroek 1984). In the soils of the igapó, total amounts of Na, K, Mg and Ca are more than one order of magnitude lower than those found in várzea soils (Furch 1997). Carbon and nitrogen contents of the soils are similar in the two ecosystems; average pH values are higher in várzea than in igapó (Furch 1997). The nutrient levels of the soils are reflected by the vegetation of the two ecosystems. In várzea, net productivity of herbaceous species (*Echinochloa polystachya*) reaches values of 100 t ha^{-1} which are among the highest recorded (Piedade *et al.* 1991). *Echinochloa polystachya* and other fast-growing macrophytes do not occur in igapó. Also fast-growing pioneer trees are almost completely lacking in igapó, while in várzea the genera *Cecropia*, *Salix*, *Senna* and others dominate the early stages of colonization. Tree height is similar in várzea and igapó, but várzea forests have considerably higher nutrient concentrations than igapó forests (Klinge *et al.* 1983), with higher biomass and higher productivity. Litterfall in várzea (10.3 t ha^{-1} y^{-1}) is considerably higher than in igapó (6.7 t ha^{-1} y^{-1}) (Worbes 1997). Compared to other Amazonian forest stands, várzea forests produce the highest and igapó forests the lowest amount of litterfall. Leaves of species from the igapó have low concentrations of nitrogen and phosphorus, and a high accumulation of structural carbohydrates (Furch & Junk 1997). In várzea, the mesophyllous leaf size-class is better represented than in igapó, where notophyllous leaves predominate, and tree leaves tend to have lower mass per unit leaf area than in igapó (Klinge *et al.* 1983). Many trees of the igapó have scleromorphic leaves and are evergreen (Worbes 1983), whereas in várzea sclerophylly is less common, and deciduousness in the period of high water levels was found to be very common. Average wood density of 30 species from várzea was 0.53 g cm^{-3}, compared to the 0.68 g cm^{-3} for 35 species from

igapó (Parolin & Ferreira 1998). Mean annual increment was considerably higher in várzea than in igapó (Parolin *et al.* 1998, Worbes 1997). Net assimilation rates of leaves are generally higher in várzea species than in igapó species (Parolin 1998). In várzea, the stress induced by periodic flooding is compensated for by morphological adaptations (Waldhoff *et al.* 1998), which require a high nutrient supply and allow the plants to maintain dynamic activities despite waterlogging. Igapó species, however, cannot 'afford' the costly production of morphological adaptations and frequent changes of leaves; their strategy is to remain in a state of rest during flooding (Parolin 1998).

In general, the environment has had a strong influence on the evolution of seed mass (Michaels *et al.* 1988, Westoby *et al.* 1992). Since nutrient resources are distinct in várzea and igapó, it might be expected that seedlings are subjected to different selective pressures for dispersal and establishment reflected by seed mass. There is a trend for infertile soils to have species that produce smaller seeds than species on fertile soils (Grubb 1996, Marañon & Grubb 1993). Species on nitrogen-poor Amazonian caatinga in Venezuela had significantly smaller seeds than the trees in adjacent forest on less infertile soils, and than trees in lowland forests elsewhere (Grubb & Coomes 1997). Not all studies, however, have found a relationship between seed size and establishment conditions (Augspurger 1984). Hammond & Brown (1995) found no significant effect of soil type on seed size in Guyana. In woody angiosperms from Manu, Peru, there was no evidence of adaptation of seed mass to habitat use, successional syndrome or growth form when taxonomic relatedness was taken into account (Kelly 1995).

This paper concentrates on the interspecific differences in seed mass in two Amazonian floodplain systems, nutrient-rich várzea and nutrient-poor igapó. The central question is whether or not the seed masses of tree species from várzea are significantly different from those of trees in igapó. A second question deals with seed mass in relation to the position of a tree species along the flooding gradient. The duration of the period of inundation depends on the position of the plant in the flooding gradient (Junk 1989), and seedlings are subjected to determined periods of submergence, which can be limiting to survival. Although seed size does not necessarily have an effect on relative survival of the seedling, seedlings from larger seeds can be favoured at early stages of growth (Wulff 1986a). Large seeds enable the early development of an enlarged resource-gathering system, i.e. roots or photosynthetic tissue (Hewitt 1998). The second question is therefore whether or not seed mass is related to the elevation at which the species occurs most often on the flooding gradient.

STUDY SITES AND SPECIES

Four study sites were chosen in várzea and igapó forests near Manaus, Brazil. For várzea, one study site was located on the Ilha da Marchantaria, a river island 15 km upstream from the confluence of the Amazon River and Rio Negro, and one in Costa do Catalão, on the Amazon River, 10 km from Manaus.

For igapó, one site was located in the lower course of Rio Tarumã-Mirim, 20 km north-east of Manaus, and one in the National Park of Rio Jaú, 200 km north-east of Manaus.

Variation of water level in the study areas is markedly seasonal. The rising phase lies between December and June, while the draining period occurs from July to November. Mean monthly temperature ranges from 26.3 – 27.2 °C. Rainfall ranges from 1700 – 2300 mm. The amount of rain is irregularly distributed throughout the year, with a dry season between June and November, and a rainy season from December – May. Species were chosen according to their abundance in each forest type, based on the available floristic inventories (Ayres 1993, Ferreira 1991, Rankin-de-Mérona 1988, Revilla 1981, Worbes 1983). The species were chosen to represent a wide array of taxa, as well as different ecological and morphological characteristics. To test the influence of the period of inundation, the chosen species were separated into two groups, according to their occurrence on the flooding gradient (Ferreira 1991, Parolin & Ferreira 1998). Species typically growing between 25 and 28 m asl were classified as 'high' on the flooding gradient (subjected to short periods of inundation). Species growing mainly between 18 and 25 m asl were classified as 'low' (subjected to long periods of inundation) on the gradient.

METHODS

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. Fruits and seeds were placed in plastic bags, transported to the laboratory, dried to constant mass at 105 °C, and weighed using an electronic balance. The Mann–Whitney U-test was used to test the differences in the dry seed mass of the two groups of species.

The classification of 'species from várzea' and 'species from igapó' (Table 1) is based on where the seeds were collected, which does not mean the species does not occur in the other ecosystem: depending on the author, the species is considered to be restricted to one of the ecosystems, to occur in both, or even to occur in terra firme (Ayres 1993, Ducke 1913, Ferreira 1991; Kubitzki 1989 a, b; Rankin-de-Mérona 1988, Revilla 1981, Rosales *et al.* 1999, Worbes 1983, Worbes *et al.* 1992).

RESULTS

In this study, fruits and seeds were analysed for 31 species from 20 families typical for várzea, and 27 species from 14 families from igapó (Table 1). In this sample eight families were represented in both várzea and igapó (Annonaceae, Caesalpiniaceae, Clusiaceae, Euphorbiaceae, Lecythidaceae, Myrtaceae, Papilionaceae, Sapotaceae), 12 in várzea alone and six in igapó alone. Two genera, *Pouteria* and *Tovomita*, were represented in both várzea and igapó among the

Table 1. Mean (±SE) fruit and seed dry masses for selected tree species of (a) várzea and (b) igapó, in alphabetical order by species. Elevation in the flooding gradient (H=high: 25–28 m asl, L=low: 18–25 m asl, – no data).

	Family	Elevation	Dry mass (g)		n
			Fruits	Seeds	
(a) Species from várzea					
1 *Annona hypoglauca*	Annonaceae	L	59.53 ± 4.15	0.440 ± 0.008	10
2 *Byrsonima chrysophylla*	Malpighiaceae	–	0.85 ± 0.05	0.425 ± 0.026	4
3 *Cecropia latiloba*	Cecropiaceae	L	25.83 ± 0.62	0.002 ± 0.000	10
4 *Cecropia membranacea*	Cecropiaceae	H	25.83 ± 0.69	0.002 ± 0.000	8
5 *Crateva benthami*	Capparidaceae	L	44.36 ± 3.70	0.205 ± 0.007	10
6 *Crescentia amazonica*	Bignoniaceae	L	10.65 ± 2.87	0.004 ± 0.000	5
7 *Crudia amazonica*	Caesalpiniaceae	L		6.378 ± 0.496	10
8 *Eschweilera ovalifolia*	Lecythidaceae	L	34.40 ± 4.008	6.663 ± 0.523	10
9 *Garcinia macrophylla*	Clusiaceae	–		0.743 ± 0.024	10
10 *Gustavia augusta*	Lecythidaceae	H	11.73 ± 0.16	0.796 ± 0.029	7
11 *Ilex inundata*	Aquifoliaceae	L	0.13 ± 0.02	0.013 ± 0.002	4
12 *Laetia corymbulosa*	Flacourtiaceae	H	0.48 ± 0.04	0.004 ± 0.000	7
13 *Lecythis* sp.	Lecythidaceae	–		4.978 ± 0.180	10
14 *Myrcia* sp.	Myrtaceae	–	0.52 ± 0.04	0.395 ± 0.030	4
15 *Nectandra amazonum*	Lauraceae	L	3.67 ± 0.20	2.032 ± 0.145	10
16 *Neolabatia cuprea*	Sapotaceae	–	6.00 ± 2.36	1.200 ± 0.104	3
17 *Piranhea trifoliata*	Euphorbiaceae	L	0.52 ± 0.02	0.055 ± 0.004	10
18 *Platymiscium ulei*	Papilionaceae	H		0.192 ± 0.013	6
19 *Pouteria glomerata*	Sapotaceae	L	8.18 ± 1.18	0.330 ± 0.005	3
20 *Pouteria stylosa*	Sapotaceae	L	3.49 ± 0.41	1.995 ± 0.039	2
21 *Poseudobombax munguba*	Bombacaceae	H	83.85 ± 17.6	0.013 ± 0.001	10
22 *Psidium acutangulum*	Myrtaceae	L	4.67 ± 0.26	0.109 ± 0.009	10
23 *Pterocarpus amazonum*	Papilionaceae	–	2.18 ± 0.28	0.400 ± 0.042	5
24 *Salacia* sp.	Hippocrateaceae	–	56.74 ± 0.56	5.488 ± 0.168	10
25 *Salacia imprensifolia*	Hippocrateaceae	–		2.155 ± 0.046	10
26 *Salix humboldtiana*	Salicaceae	L	0.01 ± 0.00	0.002 ± 0.000	7
27 *Senna reticulata*	Caesalpiniaceae	H	0.61 ± 0.02	0.013 ± 0.000	10
28 *Tabebuia barbata*	Bignoniaceae	L	9.21 ± 0.39	0.261 ± 0.032	10
29 *Tovomita* sp.	Clusiaceae	–	1.48 ± 0.14	0.270 ± 0.005	3
30 *Vitex cymosa*	Verbenaceae	L	0.41 ± 0.04	0.209 ± 0.009	10
31 *Zanthoxylum compactum*	Rutaceae	–	0.12 ± 0.01	0.080 ± 0.004	5
(b) Species from igapó					
1 *Acosmium nitens*	Caesalpiniaceae	L	0.28 ± 0.02	0.118 ± 0.006	10
2 *Aldina latifolia*	Caesalpiniaceae	H	75.92 ± 7.51	69.355 ± 8.639	10
3 *Alibertia edulis*	Rubiaceae	L	0.10 ± 0.03	0.014 ± 0.001	10
4 *Amanoua oblongifolia*	Euphorbiaceae	L	0.22 ± 0.01	0.043 ± 0.003	10
5 *Calliandra amazonica*	Mimosaceae	–	6.42 ± 0.64	0.481 ± 0.025	10
6 *Campsiandra comosa*	Caesalpiniaceae	L		6.129 ± 0.257	10
7 *Clathotropis nitida*	Papilionaceae	–	0.74 ± 0.09	0.153 ± 0.003	3
8 *Clitoria amazonum*	Papilionaceae	L	3.44 ± 0.72	0.083 ± 0.012	10
9 *Eschweilera tenuifolia*	Lecythidaceae	L	9.09 ± 0.66	3.140 ± 0.100	4
10 *Eugenia gomidesiana*	Myrtaceae	L		0.706 ± 0.024	10
11 *Hevea spruceana*	Euphorbiaceae	L	36.05 ± 2.19	4.088 ± 0.270	10
12 *Himatanthus attenuata*	Apocynaceae	L	4.00 ± 0.49	0.074 ± 0.003	10
13 *Macrolobium acaciifolium*	Caesalpiniaceae	H	3.88 ± 0.56	1.426 ± 0.432	5
14 *Maprounea guianensis*	Euphorbiaceae	L	0.08 ± 0.01	0.011 ± 0.002	9
15 *Mollia speciosa*	Tiliaceae	L	1.12 ± 0.04	0.008 ± 0.001	9
16 *Mora paraensis*	Caesalpiniaceae	H	95.64 ± 9.69	38.510 ± 3.722	10
17 *Myrtaceae* sp.	Myrtaceae	–	0.65 ± 0.09	0.208 ± 0.016	8
18 *Ormosia excelsa*	Caesalpiniaceae	L	1.83 ± 0.09	0.734 ± 0.047	5
19 *Parkia discolor*	Mimosaceae	L	11.16 ± 0.35	0.284 ± 0.007	10
20 *Poecilanthe amazonica*	Papilionaceae	H	4.52 ± 0.50	0.811 ± 0.052	9
21 *Pouteria elegans*	Sapotaceae	L		1.339 ± 0.163	10
22 *Pseudoxandra polypheba*	Annonaceae	–	1.34 ± 0.04	0.397 ± 0.015	10
23 *Sacoglottis amazonica*	Humiriaceae	–	7.32 ± 0.54	4.994 ± 0.403	10
24 *Swartzia polyphylla*	Papilionaceae	H	38.43 ± 5.75	30.236 ± 2.256	10
25 *Symmeria paniculata*	Polygonaceae	L	0.07 ± 0.01	0.017 ± 0.002	5
26 *Tovomita macrophylla*	Clusiaceae	–	10.20 ± 1.09	1.354 ± 0.193	5
27 *Vatairea guianensis*	Papilionaceae	H	30.71 ± 3.00	26.466 ± 2.085	10

Table 2. Comparison between species from várzea and igapó showing the number of analysed species and families, number of analysed families occurring only in várzea or in igapó, number of analysed species growing at high (25–28 m asl) and low (18–25 m asl) elevations, the range (and mean) of fruit and seed dry masses, in trees from várzea and igapó.

	Species from	
	várzea	igapó
Number of species	31	27
Number of families	20	14
Number of families restricted to várzea/igapó	12	6
Species of high elevation	6	6
Species of low elevation	15	15
Fruit dry mass (g)	0.006 – 83.9 (15.21)	0.073 – 95.6 (14.34)
Seed dry mass (g)	0.002 – 6.66 (1.16)	0.008 – 69.36 (7.08)

chosen trees. Following literature citations (Kubitzki 1989a, b; Prance 1979), several species occur in both systems, but seeds were not found in the chosen study sites in várzea and igapó. Therefore intraspecific comparisons cannot be made here.

Mean dry seed masses (seed weight) ranged from 0.002 – 6.66 g in the chosen várzea species, and from 0.008 – 69.36 g in igapó species (Table 2). Mean seed mass was significantly different (Mann–Whitney test: $U = 538$, $P = 0.035$) between the species of the two floodplain forest systems and almost seven times smaller in the várzea species (mean = 1.16 g, SE = 0.4) than in the igapó species (mean = 7.08 g, SE = 3.1). The distribution among seed mass classes was markedly different in the two systems. Higher seed masses (> 10 g) occurred exclusively in igapó (Figure 1).

Seed mass was not homogeneously distributed in species from different positions along the flooding gradient. In both várzea and igapó, six species occurred at high, and 15 species occurred at low, elevations (Table 2). The six tree species from higher levels (26 – 29 m asl) in igapó (*Aldina latifolia*, *Mora paraensis*, *Swartzia polyphylla*, *Vatairea guianensis*, *Macrolobium acaciifolium* and *Poecilanthe amazonica*) had significantly higher seed masses than the species from lower positions in igapó or from all positions in white-water floodplains (Figure 2). Maximum seed mass at high positions in igapó reached 69.4 g, while at mean and low positions in igapó and in várzea it did not exceed 6.7 g. Differences between igapó and várzea were not significant when considering only mean and low positions in igapó. Highly significant differences were found between high positions in igapó and the rest (mean and low positions in igapó and all positions in várzea).

Since species do not necessarily represent independent data points there is a need to take into account the effect of relatedness among species (Kelly & Purvis 1993). Comparing the eight families that were represented in both várzea and igapó (Table 3), seed mass was significantly higher in igapó in the Caesalpiniaceae, Clusiaceae, Euphorbiaceae, Myrtaceae and Papilionaceae. In particular the Caesalpiniaceae and Papilionaceae, which had big sample sizes,
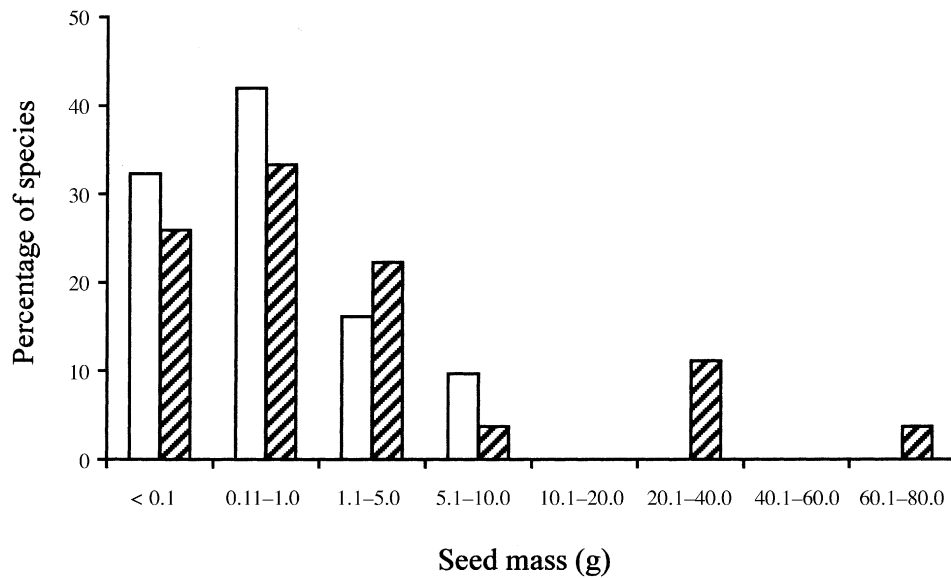
Figure 1. Distribution of seed mass classes (dry weight in g) for species from the vegetation types várzea (□) and igapó (▨) in Amazonian floodplains near Manaus, Brazil.
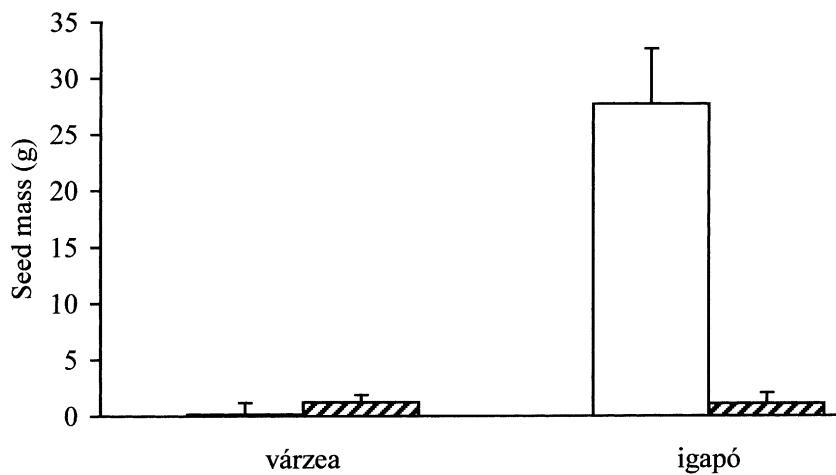

Figure 2. Mean seed mass (with SE) of species from várzea and igapó in Amazonian floodplains near Manaus, Brazil, that are typical for high (25–28 m asl, □) and low (18–25 m asl, ▨) elevations.

showed clear differences between seed mass in várzea and igapó, and also when differentiated by their occurrence in the flooding gradient (high/low). No difference was found in the Annonaceae, Lecythidaceae or Sapotaceae.

The two genera that occur in both ecosystems, *Pouteria* and *Tovomita*, showed different trends: the species of *Pouteria* did not show any differences in seed mass between várzea and igapó, the species of *Tovomita* had higher seed mass in igapó.

Table 3. Comparison of eight families represented in both várzea and igapó showing mean seed dry mass (g) ± SE and n, the number of species considered.

Family	Várzea	n	Igapó	n
Annonaceae	0.44	1	0.40	1
Caesalpiniaceae	3.19±3.18	2	19.38±11.67	6
Clusiaceae	0.51±0.21	2	1.35	1
Euphorbiaceae	0.06	1	1.38±0.94	6
Lecythidaceae	4.15±1.73	3	3.14	1
Myrtaceae	0.25±0.14	2	0.46±0.28	2
Papilionaceae	0.30±0.07	2	11.55±6.88	5
Sapotaceae	1.60±0.42	2	1.34	1

DISCUSSION

In the present study the functional group of trees from floodplains was analysed, and seed dry mass ranged over four orders of magnitude. Worldwide, seed mass ranges over ten orders of magnitude (Harper *et al.* 1970). Within Asian and Australian tropical forests, six orders of magnitude were found for tall shade-tolerant trees (Grubb & Coomes 1997).

A significant difference in mean seed mass was found in the chosen species in várzea and igapó. Compared to trends found elsewhere, it is a surprise that the seeds of igapó species are bigger or about the same size as their relatives in the várzea, rather than appreciably smaller (P. J. Grubb, *pers. comm.*). At this point it is especially important to take into account taxonomic information. When comparisons are made within the seven families occurring in both systems, they yield the same trend – as that found in the comparison made without respect to phylogeny – in six cases (Caesalpiniaceae, Clusiaceae, Euphorbiaceae, Lecythidaceae, Myrtaceae, Papilionaceae) but not in one (Sapotaceae). If species are compared within genera, *Tovomita* shows the same trend as the general data set, whereas *Pouteria* showed no convincing trend.

Although sample size was small, if there was a difference of seed mass between várzea and igapó, than it was always higher in igapó than in várzea. In some groups (the genus *Pouteria*, the families Annonaceae, Lecythidaceae and Sapotaceae) no differences were detectable. It was never found that the taxa representing the várzea had higher seed mass. When the four species with highest seed mass in igapó are excluded from the calculations, average seed mass is almost identical to that of várzea species (1.16 g in both ecosystems). These four species belong to the families of Caesalpiniaceae and Papilionaceae, which also occur in low positions in igapó and várzea, and can have very low seed mass. This indicates that the particularly high seed mass of the four abovementioned species is not a typical feature of the families they belong to, but their adaptation to the conditions at high elevations in the flooding gradient.

How can the results of this study be interpreted? Seeds of different sizes are suited to different dispersal modes, germination strategies (Haig 1996) and establishment conditions (e.g. Foster & Janson 1985, Salisbury 1942). Small

seeds are advantageous because there are fewer limits to the amount of seed production, and the higher number of seeds allows the occupation of more of the available microsites. Seedlings of large seeds are less subjected to physical disturbance by animals, damage by falling branches, litter or sediment layers, drought, darkness and soil instability (Grubb 1998, Grubb & Coomes 1997, Grubb & Metcalfe 1996, Hewitt 1998, Kelly 1995, Mack 1998, Metcalfe & Grubb 1995). Large seeds allow higher rates of seedling establishment since they have more endosperm and are richer in energy reserves for the developing embryo (Michaels *et al.* 1988, Moegenburg 1996).

It is generally agreed that seed size has evolved in relation to selection pressures at the establishment stage as well as at the dispersal stage (P. J. Grubb, *pers. comm.*). Also, dispersal might concern the fruit more than the seed, depending upon whether the attractant for animal dispersers is the fruit or the seed. It may well be that seed size and fruit size are correlated, and that it is not seed size but fruit size that is the main target for selection (Kelly 1995). In the present study, there were almost no differences between average fruit dry weight in várzea (15.2 g) and igapó (14.3 g) (Table 2). Dispersal mechanisms – mainly hydrochory (Ziburski 1990) and ichthyochory (Goulding 1980) – probably act in a similar way in várzea and igapó, which might explain why lower nutrient levels in igapó do not cause small-seededness as was often found in infertile environments (Grubb 1996, Grubb & Coomes 1997, Marañon & Grubb 1993). Also the similar seed mass at low elevations in igapó and in high plus low elevations in várzea might be explained by the similar dispersal mechanisms.

The remaining question is: why do the species that grow at high levels in the flooding gradient have higher seed masses than those species that grow at low elevations, and why is this found only in igapó, and not in várzea? In várzea, nutrient reserves are available from the environment and the need to supply the seedling with nutrients from the parental tree is small. This is not the case in igapó, where the environment provides very little in the way of nutrients and the seed resources that are particularly important for early growth of seedlings (Bazzaz & Miao 1993, Wulff 1986b) have to be supplied by the parental tree. In floodplains in particular, the time before the next flooded period is limited to few months a year (Junk *et al.* 1989) and survival rates of the seedlings will be higher if a certain height can be achieved before the onset of flooding. For species that do not tolerate complete inundation of several months, fast height growth should be considered as an adaptation for escaping total flooding. At lower levels in the flood gradient, plants cannot escape total flooding, they have to withstand it. The probability of a seedling being able to grow over the water level is low and only highly flood-tolerant species can survive. They need strategies other than fast growth to withstand flooding, e.g. physiological and morphological adaptations of the seedlings that allow them to tolerate several weeks to months of submergence. The capacity to photosynthesize under water has been postulated for some species

(Fernandes-Corrêa & Furch 1992, Schlüter 1989, Schlüter & Furch 1992) and can be of fundamental importance for survival. Other species shed their leaves, are dormant during the period of complete flooding and resprout soon after the water recedes (Parolin 1997, 1998).

At high levels in the flood gradient, the need for such adaptations is smaller and the important strategy is fast height growth. If a seedling can achieve a height of few metres before the flood, some leaves can be kept above the water surface enhancing survival, as has been shown in the várzea for *Senna reticulata*: it does not tolerate submergence but grows 4 m in 8 mo which enables survival in the highest levels of the flood gradient where it exclusively occurs (Parolin 1999). The three large-seeded species from igapó (> 30 g, *Aldina latifolia*, *Mora paraensis* and *Swartzia polyphylla*) have also been described as extremely intolerant to submergence (Kubitzki & Ziburski 1994, Ziburski 1990). They occur only at high levels, and seedlings grow to a height of 2 m without nutrients, light or water supply as observed casually in seeds that germinated on a concrete floor under a roof (P. Parolin, *pers. obs.*). This demonstrates the capacity for fast height growth, and the independence of these species from external factors in the first weeks or months after germination.

Some of the species considered to be typical for these higher positions in igapó are reported to occur also in várzea. *Macrolobium acaciifolium* and *Swartzia polyphylla* have been mentioned for both floodplain systems (Ducke 1913, Worbes 1983). *Vatairea guianensis* occurs in both floodplain systems (Worbes *et al.* 1992) as well as on terra firme (Kubitzki 1989a). *Aldina latifolia* is typical for igapó (Kubitzki 1989b), but occurs also on terra firme (W. Laurance, *pers. comm.*). Only *Mora paraensis* and *Poecilanthe amazonica* are restricted to igapó. Considering this, species with high seed mass are restricted to the higher regions in the flooding gradient due to their low flood tolerance, but are not necessarily linked to one of the floodplain systems. Also in várzea, high seed mass can bring advantages, although the need for parental nutrient supply is smaller.

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