ECOTROPICA

Volume 11 2005 No. 1-2

ECOTROPICA 11: 1–8, 2005

SEEDLING MORPHOLOGY OF NON-PIONEER TREES IN CENTRAL AMAZONIAN *VÁRZEA* FLOODPLAIN FORESTS

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Abstract. The relation between seed size, seedling morphology and germination is analyzed for 11 non-pioneer tree species typical of Amazonian *várzea* floodplain forests. A classification of seedling morphology and establishment strategies is presented. Seeds were collected in the field (*várzea*), put into plastic bags and transported to the INPA (Amazon Research Centre, Manaus, Brazil) where they were planted under semi-natural conditions. The seedlings were classified according to seed weight and size (length x width) and the position and function of their cotyledons. Four main types of seedlings were found: cryptocotylar hypogeal with reserve or absorption cotyledons (CHR), phanerocotylar epigeal with foliaceous (photosynthetic) cotyledons (PEF), phanerocotylar epigeal with reserve cotyledons (PER), and phanerocotylar hypogeal with reserve cotyledons (PHR). The most frequent seedling type was PEF (followed by CHR, PHR, and PER), which also had the smallest seeds and the highest germination percentages. Small seeds germinated earlier, also within a germination type. Although 11 tree species represent only a very small percentage of the species occurring, some trends can be shown which perhaps are found also in other trees of the *várzea* forest. It may be expected that the dominance of PEF seedlings in *várzea* is not a coincidence: in the nutrient-rich *várzea* environment the presence of nutrient-supplying cotyledons is not as important as in nutrient-poor environments. A newly established seedling can get nutrients from the soil, and foliaceous photosynthetic cotyledons are sufficient for fast initial growth. Nevertheless, taken together the species with reserve cotyledons accounted for almost 64 % of the analyzed species. These reserve cotyledons enhance fast growth in an environment with extreme flooding conditions and thus with a reduced period of favorable conditions for establishment.
Accepted 9 February 2005.

Key words: *Amazonia*, *establishment*, *floodplain forest*, *germination*, *seedling type*, *seed size*.

INTRODUCTION

In Amazonian floodplain forests, seedling establishment is a particularly critical stage given the extreme situation caused by regular floodings for up to 210 days every year and a water column of 10–15 m (Junk 1989). Seedling emergence and establishment are always critical life-cycle stages (Hladik & Miquel 1990, Harper 1997, Ibarra-Manríquez *et al.* 2001) and the environment has a strong influence on their evolution (Michaels *et al.* 1988, Westoby *et al.* 1992). Seed size, dispersal capacity, and establishment are associated with the initial morphology of seedlings (Ng 1978, Foster *et al.* 1986) and are important factors in determining seedling growth and survival. The number of days to germination is often positively related to seed size (Ng 1973), and smaller seeds may be less successful in establishment (Ganeshaiah & Shaanker 1991). Early successional or pioneer species will generally have smaller and lower seed weights than those of late successional or persistent species and grow quickly in light-rich environments (Salisbury

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1974, Ng 1978). The morphological features in seedling development and establishment, seed dispersal and successional status have been analyzed in several studies performed in tropical non-flooded rain forests (e.g., Alencar & Magalhães 1979, Silva *et al.* 1988, Hladik & Miquel 1990, Armstrong & Westoby 1993, Bazzaz & Miao 1993, Moreira & Wessen 1996, Agyeman *et al.* 1999, Poorter 1999, Kitajima 2003). However, our knowledge about seedling establishment in Amazonian floodplain forests is small despite the high number of trees which are endemic there. The few studies which are available (Ziburski 1991, Kubitzki & Ziburski 1994, Maia & Jackson 1998, Parolin 2000, 2001; King 2003, Wittmann & Junk 2003) indicate that the high tree species diversity in the floodplains is accompanied by a high variety of establishment strategies.

We believe it important to analyse initial seedling morphology and establishment strategies also as a basis for potential reforestation. Although many tree species of Central Amazonian floodplains have a high ecological value as food resources for fish (Kubitzki & Ziburski 1994, Maia 1997, 2001; Waldhoff & Maia 2000), or commercial value for timber and other forest products, little is known about them. Thus in this paper we investigate seedling morphology of 11 non-pioneer tree species from Central Amazonian whitewater floodplain forests (*várzea*). We describe the seedling types on the basis of the position (length of hypocotyls), exposure (cotyledons covered or uncovered by seed coat), and function of cotyledons as mainly photosynthetic or storage organs, and the relationship between seedling type, and seed size, and between seedling morphology and the time to germination as well as the germination percentage. We address the following questions: (i) Do seedling types vary among species differing in seed size?; (ii) Is seedling size associated with the number of days to germination and with germination percentage?; (iii) Does the nutrient-rich whitewater floodplain (*várzea*) favor a specific seedling type over others?

MATERIAL AND METHODS

Plant material and study area. Eleven species from Central Amazonian floodplain forests were chosen (Table 1). These species are common in the floodplain forests and can be considered as non-pioneer trees of higher successional stages. Seeds were collected in the field, put into plastic bags and transported to the

TABLE 1. Species studied, seedling morphology, time to germination, germination percentage, and seed size.

Type	Species	Family	Time to germination (days) of > 50% seeds and number of seeds planted (n)	Germination (%)	Germination of first and last seed (days)	Seed area (cm^2)
PEF	*Annona hypoglauca*	Annonaceae	30 (n = 100)	60	20–120	5,12 ± 0,6
	Bothriospora corymbosa	Rubiaceae	7 (n = 400)	100	4–12	0,03 ± 0,001
	Crescentia amazonica	Bignoniaceae	8 (n = 500)	95	5–15	0,28 ± 0,07
	Pseudobombax munguba	Bombacaceae	7 (n = 200)	100	5–12	0,2 ± 0,08
			MEAN	**88,8**		**1,4**
PER	*Cassia leiandra*	Fabaceae	7 (n = 50)	70	5–20	3,6 ± 1,0
	Crateva benthami	Capparaceae	8 (n = 100)	90	10–20	0,72 ± 0,3
			MEAN	**80,0**		**2,2**
PHR	*Macrolobium acaciifolium*	Fabaceae	25 (n = 500)	90	13–49	12 ± 3,4
	Sorocea duckei	Moraceae	10 (n = 200)	83	12–25	1,32 ± 0,2
			MEAN	**86,5**		**6,7**
CHR	*Nectandra amazonum*	Lauraceae	21 (n = 20)	85	27–35	4,8 ± 0,6
	Garcinia brasiliensis	Clusiaceae	28 (n = 50)	83	25–45	3,08 ± 0,9
	Vitex cymosa	Verbenaceae	7 (n = 100)	95	2–10	0,84 ± 0,1
			MEAN	**87,7**		**2,9**

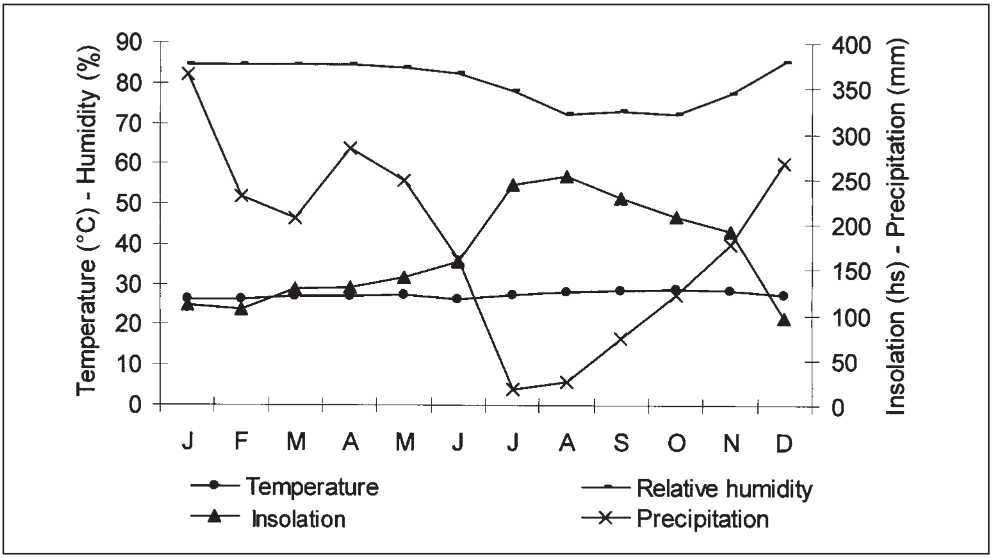

FIG. 1. Monthly mean relative air humidity (%) and temperature (°C), and sum of insolation (hs) and precipitation (mm). Data provided by the Agriculture Station Manaus-AM, from January 2000 to December 2001.

laboratory for planting. The study area was a 2-ha forest plot in a *várzea* forest, Lago Camaleão on the Ilha da Marchantaria, Rio Solimões (3°15'S, 59°58'W, approximately 20 km from the city of Manaus). The climate of the area is hot and humid with monthly minimum mean temperatures ranging from 22.9 to 23.8°C, and a maximum from 30.2 to 33.3°C. Relative humidity of the air varied from 75.6% to 86.7%. Precipitation ranges from 1000 to 2500 mm. The botanical identification of the species was made by comparison with specimens from the herbarium of INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus).

Seed size and germination. The seeds were directly extracted from the mature fruits, washed after removing the pulp, and counted, measured and placed on trays which contained washed sand as a substrate, at a depth of 0.5 to 1 cm, for germination. A total of 20 to 500 seeds per species were collected, measured and planted (see Fig. 4 for exact number per species).

We measured seed size as seed area along its longest two axes (length x width). The tray was deposited in the undergrowth of a secondary forest in upland *terra firme* on the campus of the INPA, thus being subjected to the temperature, humidity, precipitation and light of the environment (Fig. 1).

The substrate was maintained humid by daily irrigation. The seeds were considered as germinated when a radicle was visible. Germination percentage was calculated by the relation PG = (SG * 100)/ ST, with PG = percent germination, SG = seeds germinated, ST = total number of planted seeds. Germination was monitored at 24-h intervals until no new germination was observed for at least one week (Oliveira & Maia 2002, Santos & Maia 2003).

Classification of seedling types. Seedlings were classified according to the position (length of hypocotyls), exposure (cotyledons covered or uncovered by seed coat), and function of cotyledons as mainly photosynthetic or storage organs, following the classification proposed by Garwood (1983, 1996) and Miquel (1985, 1987).

RESULTS

We found four types of seedlings (Fig. 2): cryptocotylar hypogeal with reserve storage or absorption cotyledons (CHR), phanerocotylar epigeal with foliaceous (photosynthetic) cotyledons (PEF), phanerocotylar epigeal with reserve storage or absorption cotyledons (PER), and phanerocotylar hypogeal with reserve cotyledons (PHR). The most common seedling type was

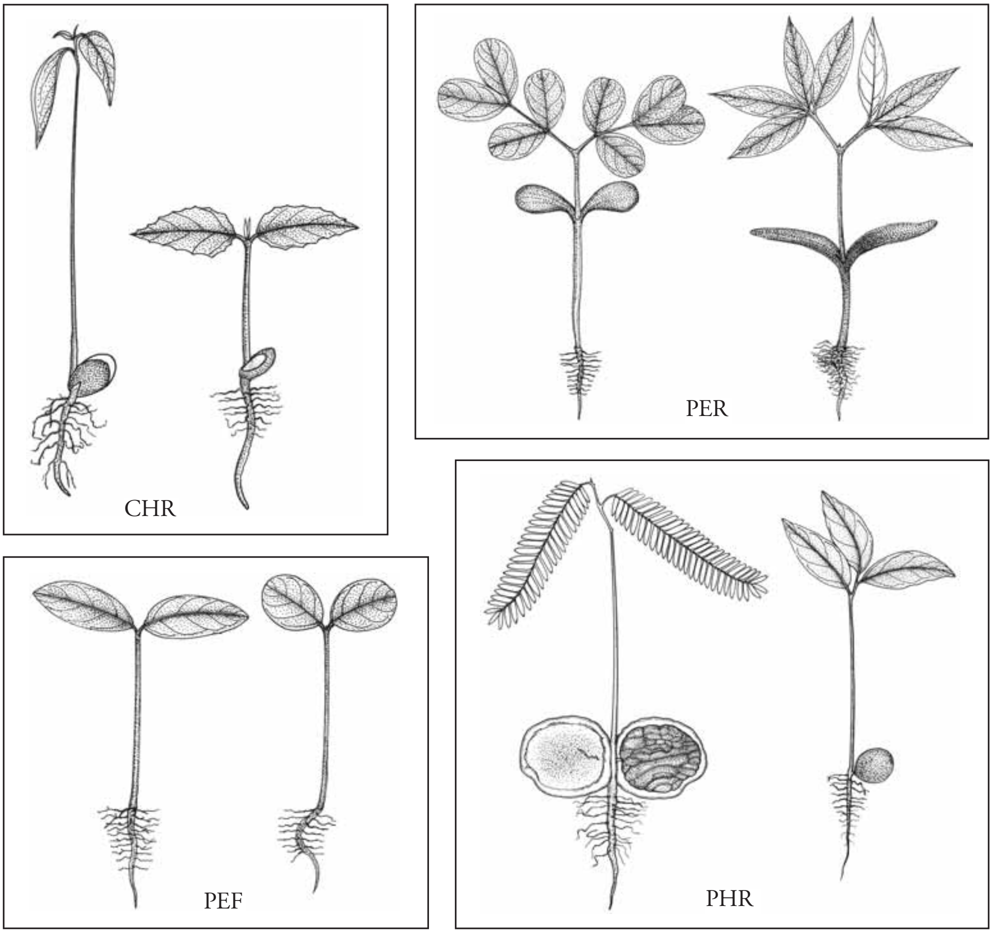

FIG. 2. Drawings of seedling morphological types: CHR, cryptocotylar hypogeal with reserve cotyledons: *Nectandra amazonum*, *Garcinia brasiliensis*, *Vitex cymosa*; PEF, phanerocotylar epigeal with foliaceous (photosynthetic) cotyledons: *Annona hypoglauca*, *Bothriospora corymbosa*, *Crescentia amazonica*, *Pseudobombax munguba*; PER, phanerocotylar epigeal with reserve cotyledons: *Cassia leiandra*, *Crateva benthami*; PHR, phanerocotylar hypogeal with reserve storage cotyledons: *Macrolobium acaciifolium*, *Sorocea duckei*.

the foliaceous PEF with 36.4 % (Fig. 3), followed by the seedling types with cotyledons functioning as reserve organs, CHR, PHR and PER, with 63.6 % (7 species) together.

The PEF seedlings had the smallest seeds (Table 1; mean 1.4 cm^2, with the overall smallest seed the 0.03 cm^2 of *Bothriospora corymbosa*) and the highest germination percentages. The PHR seedlings had the largest seeds (mean 6.7 cm^2, with the largest being *Macrolobium acaciifolium* at 12 cm2; PER had a mean of 2.2 cm^2, CHR of 2.9 cm^2). The lowest germination percentages were found in the PER seedlings, although overall germination percentages were high in all seedling types (PEF 88.7 %, PER 80 %, PHR 86.5 %, and CHR 87.6 %), independent of seed size (Table 1).

Seed germination over time in the 11 species and four seedling types is shown in Fig. 4. Small seeds germinated earlier, also within a germination type. For example in PEF, *B. corymbosa* (seed size 0.03 cm^2), *P. munguba* (0.20 cm^2) and *C. amazonica* (0.28 cm^2) ger-

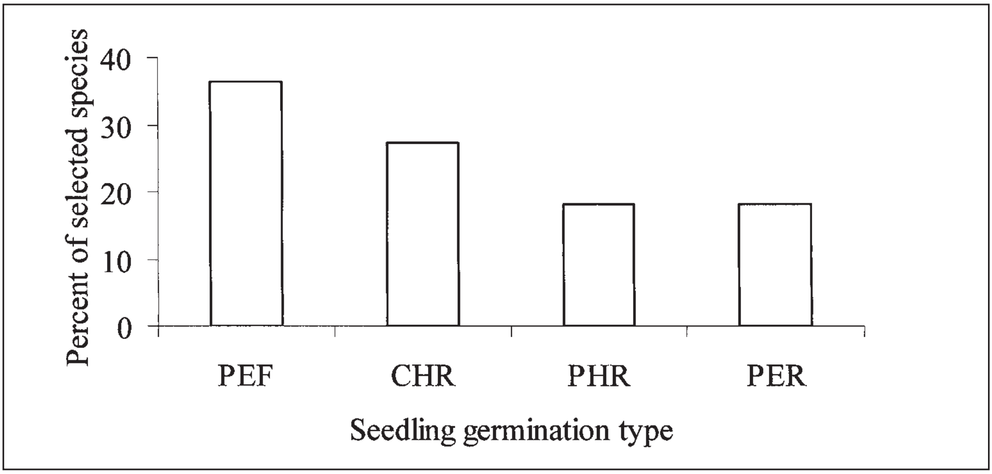

FIG. 3. Distribution of seedling morphological types among the selected species: CHR cryptocotylar hypogeal with reserve cotyledons; PEF phanerocotylar epigeal with foliaceous (photosynthetic) cotyledons; PER phanerocotylar epigeal with reserve cotyledons; PHR phanerocotylar hypogeal with reserve storage cotyledons.

minated earlier than the larger seeded *A. hypoglauca* (5.12 cm^2). In CHR, *V. cymosa* (0.84 cm^2) germinated earlier than *N. amazonum* (4.8 cm^2) and *R. brasiliensis* (3.08 cm^2), and in PHR the smaller seeded *S. duckei* (1.32 cm^2) germinated earlier than *M. acaciifolium* (12.0 cm^2). Only in PER was there no clear variation between the two species despite the differences in seed size (*C. leiandra* 3.6 cm^2 and *C. benthami* 0.72

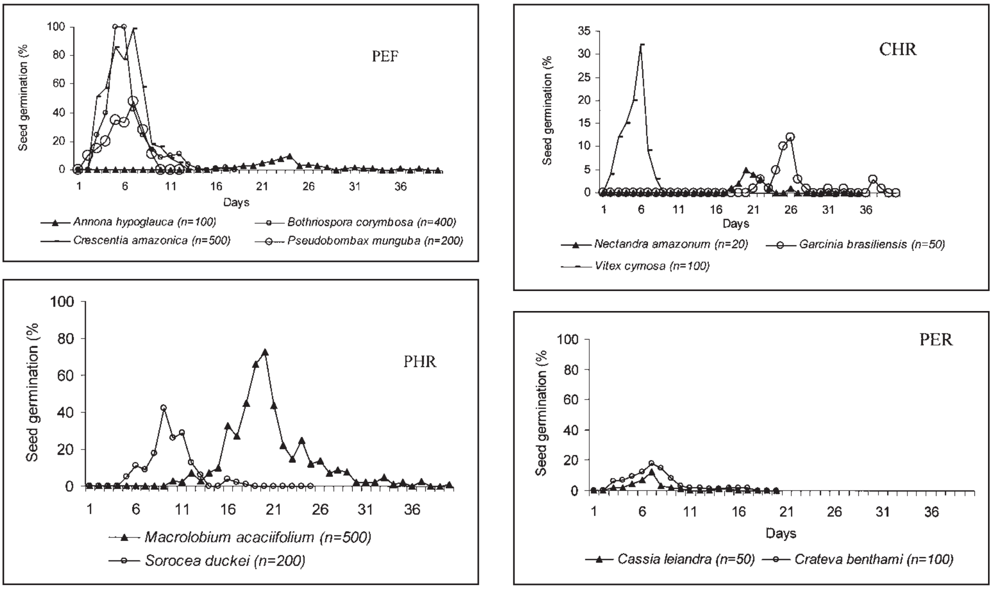

FIG. 4. Seed germination over time in the 11 species and four seedling types.

cm^2). The small seeds (> 0.03 = 1.3 cm^2) needed 7.8 days on average to germinate while larger seeds (> 3 = 12 cm^2) needed 22.2 days (Table 1).

DISCUSSION

Among the analyzed species, we found a dominance of seedlings of the phanerocotylar epigeal type with foliaceous (photosynthetic) cotyledons (PEF), although the other seedling types were also represented by more than one species each. Taken together the species with reserve cotyledons accounted for almost 64% of the species analyzed.

Although 11 species are not representative of the total number of species (about 100 species, Worbes 1997), these 11 are very common and dominating, and we think that it is possible that these trends are also found in the other trees of the *várzea* forest. There are different seedling establishment strategies which we assume to differ between habitats and ecosystems, related to the environmental conditions. The high number of PEF seedlings in *várzea* may be linked to the nutrient-rich environment. A newly established seedling can easily obtain nutrients from the soil and foliaceous photosynthetic cotyledons are sufficient for fast initial growth, allowing a fast and effective utilization of irradiation for rapid growth. PEF seedlings are common in tropical forests, especially in early successional stages and in small-seeded species, which are less competent in stability and produce less vigorous seedlings (Marshall 1986). The later successional stages frequently have reserve cotyledons, which enhance fast growth in an environment with extreme flooding conditions and thus with a reduced period of favorable conditions for establishment. Here, large-seeded species may have better initial survival probabilities, allowing higher rates of seedling establishment since they have more endosperm and are richer in energy reserves for the developing embryo (Michaels *et al.* 1988, Armstrong & Westoby 1993, Moegenburg 1996). The forest examined in this study is extremely nutrient rich but offers only a narrow window for establishment. These environmental conditions are likely to have favored species with fast germination and high growth rates.

As a contrast, in nutrient-poor environments like the *igapó* of black water rivers, initial nutrient supply by the mother tree via reserve storage in cotyledons is more crucial for survival. As a study with other seedlings showed (Parolin 2001), germination percentages and duration were lower in species from *várzea* than from *igapó* and the cotyledons opened later and had lower longevity in *várzea*, where the environment provides sufficient nutrients to the establishing seedling and there is less need for nutrient supply by the mother plant. More species have to be studied in order to analyze seedling type distributions in different Amazonian environments.

Seedling types varied among species differing in seed size, and seedling size was positively associated with the days to germination but not with germination percentages (Table 1). Mean germination percentage was above 80% in all studied species, independent of seed size. These data are similar to those described by Ziburski (1991) for most species, but higher than in Ziburski's study for the three CHR species (Ziburski 1991/present study: *N. amazonum* 65/85%, *G. brasiliensis* 38/83%, and *V. cymosa* 20/95%). In Ziburski's study, *A. hypoglauca* germinated only after submergence or passage through a fish digestive system, whereas in our study this species germinated in 60% of cases.

The parameters analyzed do not allow us to understand the mechanisms of establishment in the field. They can merely give hints that help to explain the clear species zonation along the flooding gradient and the differential occurrence of species in ecosystems with different nutrient availabilities. The establishment strategies of different seedling species and their differing tolerance of submergence result in a clear species zonation along the flooding gradient (Ferreira & Stohlgren 1999, Wittmann & Junk 2003). In Manaus, where two ecosystems – nutrient-rich *várzea* and nutrient-poor *igapó* – occur very close together, species are subjected to exactly the same climatological and hydrological conditions, but species composition and ecophysiological features are clearly distinct (Prance 1979; Parolin 2000, 2001). Overall average seed mass was higher (mean = 7.08 g) in nutrient-poor *igapó* ('seasonal *igapó*' *sensu* Prance 1979) than in nutrient-rich *várzea* (mean = 1.16 g) (Parolin 2000). Seed mass was higher in *igapó* species growing at high levels in the flooding gradient than at low levels (Parolin 2000). Nevertheless, few species were analyzed in the studies mentioned and we are still far from a good overview of the variety of establishment strategies.

ACKNOWLEDGEMENTS

This study was realized in collaboration between the National Amazon Research Institute (INPA) / Manaus, Brazil and the Max-Planck-Institute for Limnology / Plön, Germany. We thank the technicians of the CPBO/INPA, José Guedes, José Ramos and Filipe França.

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