

Germination in four low-várzea tree species of Central Amazonia

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Abstract

Trees of Central Amazonian white-water (várzea) forests are highly adapted to the annual inundations, which can last up to 7 months every year. Many trees synchronize fruit production to the period of highest water levels of the rivers, and hydrochory is especially common in species that colonize the low-lying flood-levels flooded for longer periods. The effect of the contact of diaspores with the river water is controversially discussed in literature. While many studies describe that flooding breaks the dormancy in seeds of many várzea tree species and is necessary for germination, other studies mention that seed buoyancy and/or submergence have negative effects on germination. Therefore, the present study was designed in order to test experimentally how seed buoyancy and seed submergence affect germination in four várzea tree species of the low-lying flood-levels. The tested species with buoyant seeds were *Salix martiana* and *Pseudobombax munguba*, those with submerged seeds *Laetia corymbulosa* and *Vitex cymosa*. 50 seeds from each species were (a) placed in water during a period of 15 days and afterwards moved to várzea substrate, thus simulating seed buoyancy and/or submergence in the natural environment, and (b) directly placed in várzea substrate, with four repetitions, respectively. Three species showed significantly higher percentages of germination in the flooded seeds than in the non-waterlogged seeds, while fruit-fibre involved seeds of *P. munguba* showed an opposite trend. In *L. corymbulosa*, germination initiated earlier in the submerged than in the control seeds, whereas there was no difference in the start of germination between waterlogged and non-waterlogged seeds of the other species. From buoyant seeds of *P. munguba* and *S. martiana*, seedlings with entirely formed cotyledons were developed while still in water. These seedlings were characterized by morphological differences in comparison to seedlings originating from non-waterlogged seeds and could not protrude the root into the soil (i.e. establish) when placed in the substrate. It is likely that the seed involving fruit-fibres contribute to long-distance dispersal in these species in the natural environment, and to stabilize seedlings when diaspores land on substrate. Concluding, contact with the river water did not disturb but on the contrary enhanced germination in the four studied species.

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1. Introduction

Amazonian várzea forests are subjected to periodic inundations of sediment loaded, nutrient-rich white-water rivers originating from the Andean foothills (Prance, 1979). The water-level fluctuations result in the existence of an aquatic and a terrestrial phase during the course of the year (Junk et al., 1989). Inundation of trees in highly inundated sites of the low várzea can reach heights of up to 7 m, corresponding to an inundation period of up to 230 d year⁻¹ (Wittmann et al., 2002).

The adaptation strategies of várzea trees to the prolonged inundations are well documented, such as phenological reactions (e.g., Wittmann and Parolin, 1999; Parolin et al., 2002a), reductions of the photosynthetic activity (Parolin, 2001; Fernandez et al., 1999; Waldhoff et al., 1998) and wood growth (Worbes et al., 1992; Worbes, 1997) during the aquatic phases, anaerobic metabolism (Fernandes-Corrêa and Furch, 1992; Schlüter et al., 1993), and the formation of adventitious roots (Worbes, 1986; Wittmann and Parolin, 2005).

Hydrochory by means of the river water is common in several várzea tree species (Gottsberger, 1978; Goulding, 1983; Pires and Prance, 1985; Ziburski, 1991; Kubitzki and Ziburski, 1994; Mannheimer et al., 2003). In the hydrochoric species, fruiting is synchronized to the seasonal water-level oscillations, reaching its peak during the period of highest water levels (Goulding, 1980; Ayres, 1993; Wittmann and Parolin, 1999; Parolin et al., 2002a; Schöngart et al., 2002). After dropping

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into the water, the diaspores are subjected to varying periods of buoyancy and/or submergence; they may float for at least 2 months (Kubitzki, 1985). The contact with the water surface is interpreted to be the most important factor breaking seed dormancy in the hydrochoric várzea tree species (Ziburski, 1991; Scarano, 1998). Seed buoyancy and/or submergence increase the distance covered by the river current and increase the probability of seed predation by fish and other aquatic dispersers (Goulding, 1983; Ziburski, 1991). On the other hand, submergence prevents the seeds from oxygen supply that is necessary for respiration and to initiate germination in most species (Frankland et al., 1987; Kozłowski and Pallardy, 1997) although genotype-seeds of some várzea tree species are able to germinate and to emit radicles when still buoyant and/or submerged (Ferreira, 2002; Parolin and Junk, 2002; Scarano et al., 2003). The seeds of *Pachira aquatica* (Bombacaceae) and *Hevea brasiliensis* (Euphorbiaceae) start to germinate when still floating (Kubitzki, 1985), but the emission of the epicotyl in these species was inhibited. However, Oliveira (1998) observed the formation of fully developed seedlings from buoyant seeds of the central Amazonian várzea species *Salix martiana*.

It is not clear whether the contact with water affects germination and seedling formation in buoyant and/or submersed seeds of trees in Amazonian várzea. Therefore, the present study was designed in order to test experimentally if seed buoyancy and seed submergence affect germination and seedling formation in four tree species occurring at the lowest flood-levels of Amazonian várzea forests.

2. Material and methods

2.1. Species selection

Four tree species were selected: *S. martiana* Leyb. (Salicaceae), *Pseudobombax munguba* (Mart. and Zucc.)

Dugand (Bombacaceae), *Laetia corymbulosa* Spruce ex. Benth. (Flacourtiaceae) and *Vitex cymosa* Bert. ex Spreng. (Verbenaceae). The selected species are common in central Amazonian várzea (Worbes et al., 1992; Schöngart et al., 2002; Wittmann et al., 2004), and occur with high abundances near the lowest tree establishment border, which is located at flood-levels of about 7 m (mean flood duration about 230 d year⁻¹; Wittmann et al., 2004).

Fruit production in all species occurs during the period of highest water levels (May–August, Wittmann and Parolin, 1999; Parolin et al., 2002a). Dispersal units in *S. martiana* and *P. munguba* are the seeds, which are produced in large quantities, and which are comparatively small and light. The seeds normally disperse aggregated and embedded in hairs (fibres) originating from the fruits (Fig. 1), and they are buoyant. Dispersal units in *L. corymbulosa* and *V. cymosa* are berry fruits, which contain only one seed. The fruits of *L. corymbulosa* sink when fallen into the water, whereas the fruits of *V. cymosa* float. In both species, however, the seeds sink when separated from the fruits.

2.2. Collection and germination experiments

Mature fruits were collected in low-várzea forests near the city of Manaus, at the Ilha da Marchantaria (3°15'S/60°00' W) and within the districts of Careiro (3°16'S/59°59'W) and Iranduba (3°17'S/60°03'W), lower Solimões River, central Brazilian Amazon, in June 2001. Maturity was easily recognizable due to changes in exocarp coloration. To increase the possibility of genetic variety within the sampled species, fruits were collected from three individuals that were located >15 km apart from each other.

The position of the selected trees within the flooding gradient was derived comparing flood marks of the last high-water period (2000) on the trunks with water levels recorded in



Fig. 1. Fruit (A) and mature seeds of *P. munguba* wrapped in cotton-like fibres (B).

Manaus (Engenharia dos Portos). Only individuals that occurred where mean flooding height is >6 m (flooding > 200 d year⁻¹) were selected. The fruits were transported in transparent plastic bags to the National Institute for Amazonian Research (INPA), Manaus. Germination experiments were conducted in a greenhouse at the INPA, at 80% of natural solar radiation intensity. Air temperatures ranged between 23 °C and 35 °C (mean: 29.8 °C), water and soil temperatures between 22.3 °C and 30.1 °C (mean: 28.9 °C).

The fruits of *L. corymbulosa* and *V. cymosa* opened immediately after collection, whereas the fruits of *S. martiana* and *P. munguba* opened 1 and 2 days after collection, respectively. The seeds were separated from the fruits, joined, mixed, and subsequently split into samples containing 50 seeds each.

The samples were placed in aluminium trays with sizes of 40 cm × 20 cm × 15 cm (see also Fig. 2). The trays contained (a) tap water (water column: 10 cm, changed at weekly intervals) and (b) várzea substrate. After 14 days, the samples placed in tap water were removed to trays containing várzea substrate, thus standardizing the environmental conditions for all species, and simulating a restricted period

of waterlogging of the diaspores. In order to test if the presence of seed-embedding fruit fibres influences germination in *S. martiana* and *P. munguba*, we repeated the germination experiment with additional samples: fibre-embedded seeds placed (a) in tap water (14 days) and (b) placed directly in várzea substrate.

All treatments were conducted with four repetitions, totalling each 500 seeds in *L. corymbulosa* and *V. cymosa*, and 1000 seeds in *S. martiana* and *P. munguba*.

Germination initiation and rates were determined from the emission of cotyledons, because the emission of radicles could not be monitored in the seeds placed in várzea substrate without influencing the seedling. Germination rates were recorded daily until all species had germinated, for a period of 84 days. Non-germinated seeds were observed until day 150 after the start of the experiments. After that, fungi infested all remaining seeds, and the experiments were stopped.

Temporal and quantitative variations in germination initiation, rates and end between waterlogged and non-waterlogged treatments, and between uncovered and fibre-embedded seeds were quantified by multivariate *t*-tests.

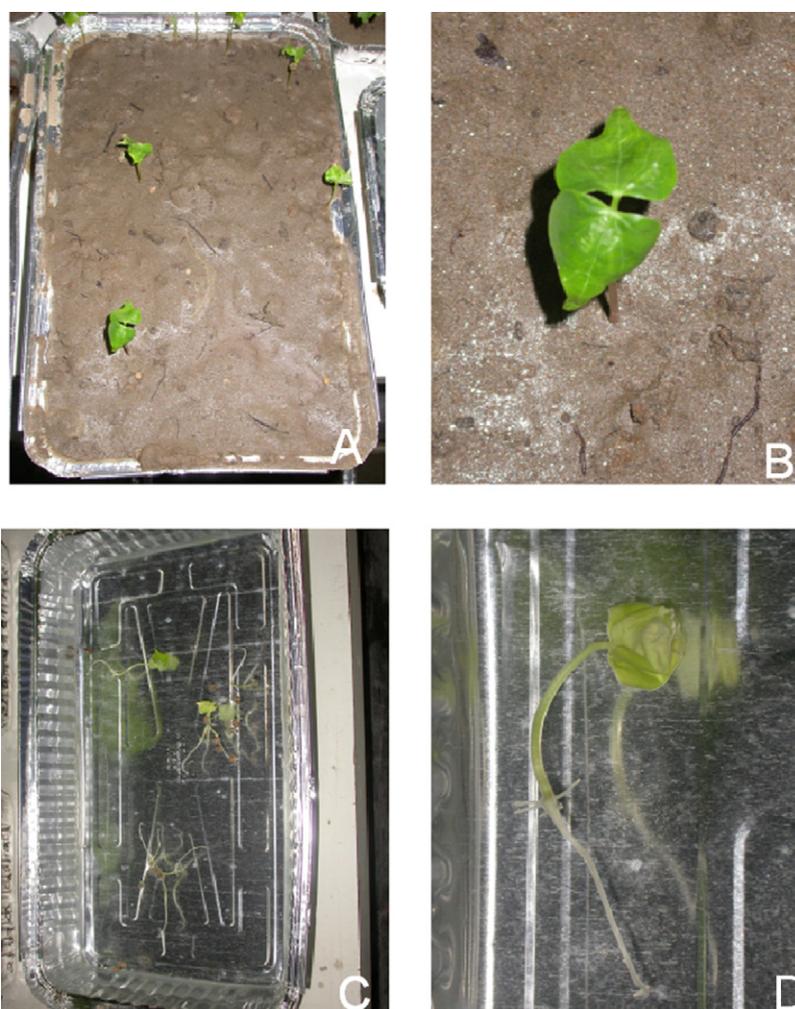


Fig. 2. Seedlings of *P. munguba* developed in soil (A and B) and from buoyant seeds in water (C and D), showing also the experimental setting.

3. Results

3.1. Initiation, rates and periods of germination

Germination in *S. martiana*, *P. munguba* and *V. cymosa* initiated after 1, 5, and 18 days, respectively, and there were no significant differences in the start of germination between waterlogged and non-waterlogged seeds, or between fibre-embedded and uncovered seeds. In *L. corymbulosa*, germination initiated after 35 days in the waterlogged seeds, and after 44 days in the non-waterlogged seeds (Table 1).

All the studied species showed significantly higher germination rates in the waterlogged than in the non-waterlogged seeds, with exception of fibre-embedded seeds of *P. munguba* (Table 2). In *V. cymosa* and *L. corymbulosa*, after 84 days, germination rates in waterlogged seeds amounted to $52 \pm 6\%$ and $39 \pm 8\%$, respectively, but only to $33 \pm 3\%$ and $6 \pm 2\%$ in the non-waterlogged seeds. In *S. martiana*, germination rates amounted to almost 100 % in all buoyant seed types, with and without embedding fruit-fibres. Germination rate in the non-waterlogged samples was minor, hereby being significantly higher in the uncovered ($80 \pm 8\%$) than in the hair-embedded ($51 \pm 4\%$) seeds (Tables 2 and 3).

In the uncovered seeds of *P. munguba*, germination rates amounted to $90 \pm 11\%$ in the buoyant and $68 \pm 7\%$ in the non-waterlogged samples. An opposite behaviour was recorded in fibre-embedded seeds: germination percentages were significantly higher in the non-waterlogged ($84 \pm 9\%$) than in the buoyant ($61 \pm 8\%$) samples (Tables 2 and 3).

In *S. martiana*, germination stopped already after 14 days in all treatments. In *P. munguba*, germination stopped after 15 days in the buoyant seed types and after 24 days in the non-waterlogged samples, without differences between presence and absence of seed embedding fruit-fibres. The submerged seeds of *V. cymosa* stopped germination after 59 days, whereas germination concluded after 66 days in the non-waterlogged seeds. In *L. corymbulosa*, germination stopped after 84 days in both treatments, submerged and non-waterlogged seeds (Table 1).

3.2. Germination type and the formation of seedlings

In all selected species, seedlings were phanerocotyledonous and epigeal according to the classification of Miquel (1987). *S. martiana* and *P. munguba* developed seedlings in both treatments, fibre-embedded and uncovered seeds, and emitted radicles followed by the development of cotyledons and primary leaves. Seedlings of all species developed in water were morphologically different from those developed on substrate. The stalks were strongly warped, and cotyledons and primary leaves were characterized by a green-yellowed coloration (Fig. 2). After the seedlings had been moved to the substrate, these were not able to protrude their roots into the substrate and died.

4. Discussion

In the four investigated tree species, buoyant and/or submerged seeds showed higher germination rates as compared to non-waterlogged seeds. In one investigated species (*L. corymbulosa*) submerged seeds started germination earlier when in water. Thus, waterlogging did not disturb but on the contrary enhanced germination indicating that buoyancy and seed submergence tolerance is an important adaptation of the investigated trees to periodical inundations, enhancing both hydrochoric dispersal and establishment.

Independent from inundation, all experiments performed in the present study showed that germination started early, at the most during the second week of observation. Seed longevity in wet tropical rainforest trees generally is comparatively short, and most trees have non-dormant seeds (Ng, 1978; Miquel, 1987; Lopez, 2001). However, dormancy is common in many Amazonian floodplain trees, where the contact of diaspores with river water is interpreted to be a crucial factor breaking seed dormancies (Ziburski, 1991; Scarano, 1998), including both fruit-dispersed and seed-dispersed species.

McHargue and Hartshorn (1983) stated that fast epicotyl growth favours seedling establishment and survival by avoiding full submersion and its consequent induction of anoxic stress during the following wet season. Although tall epicotyls may survive in várzea areas where flooding is shallow, this is

Table 1
Start and end of germination, significance, and temporal variance (F) between the treatments W = seeds positioned in tap water for a period of 14 days and afterwards moved to várzea substrate, and S = seeds positioned directly in várzea substrate

	Start of germination (day)		t-Value	p	F-ratio variance	End of germination (day)		t-Value	p	F-ratio variance
	W	S				W	S			
<i>V. cymosa</i>	18 ± 1	18 ± 1	-0.56	0.59	2.57	59 ± 2	66 ± 1	-2.55	0.03	0.89
<i>L. corymbulosa</i>	35 ± 1	44 ± 1	-9.59	0.001	1.00	84 ± 1	84 ± 1	0	1.00	2.67
<i>S. martiana</i>										
Uncovered seeds	1 ± 0	1 ± 0	-	-	-	14 ± 1	14 ± 1	-0.43	0.68	2.67
Hair-embed seeds	1 ± 0	1 ± 0	-	-	-	14 ± 1	14 ± 1	-0.43	0.68	2.67
<i>P. munguba</i>										
Uncovered seeds	5 ± 1	5 ± 1	0.43	0.68	0.37	15 ± 1	24 ± 1	-8.70	0.001	1.36
Hair-embed seeds	5 ± 0	5 ± 1	0.36	0.72	0.09	15 ± 1	24 ± 1	-9.59	0.001	8.60

Each treatment represents 250 (=5 × 50) seeds.

Table 2

Germination rates, significance, and variance between the treatments W (seeds positioned in tap water for a period of 14 days and afterwards moved to várzea substrate) and S (seeds positioned directly in várzea substrate) after 14 and 84 days in the studied species

	Germination rate after 14 days (%)		<i>t</i> -Value	<i>p</i>	<i>F</i> -ratio variance	Germination rate after 84 days (%)		<i>t</i> -Value	<i>p</i>	<i>F</i> -ratio variance
	W	S				W	S			
	<i>V. cymosa</i>	0				0	–			
<i>L. corymbulosa</i>	0	0	–	–	–	39 ± 8	6 ± 2	7.63	0.01	2.01
<i>S. martiana</i>										
Uncovered seeds	96 ± 3	80 ± 8	4.48	0.01	3.50	Ident.	Ident.	Ident.	Ident.	Ident.
Hair-embed seeds	98 ± 5	51 ± 4	9.78	0.001	39.89	Ident.	Ident.	Ident.	Ident.	Ident.
<i>P. munguba</i>										
Uncovered seeds	90 ± 11	42 ± 7	7.39	0.001	3.77	Ident.	68 ± 7	3.11	0.01	4.54
Hair-embed seeds	61 ± 8	41 ± 7	4.15	0.01	1.36	Ident.	85 ± 9	–5.16	0.001	1.03

Each treatment represents 250 (=5 × 50) seeds. Ident. = no changes between 14 and 84 days of treatment.

unlikely to be the case in areas where flooding is up to 7 m deep (Parolin, 2001). In such cases, flood-tolerance strategies at the metabolic level are likely to maintain seedling life during full submersion (Scarano et al., 1997).

In *S. martiana* and *P. munguba*, fully developed seedlings showing the emission of radicles, cotyledons and primary leaves were formed from buoyant seeds. Despite the morphological differences compared with seedlings developed on substrate, and despite the mortality of all seedlings that had germinated in our experiment, seedlings resulting from buoyant seeds may successfully establish when they land on substrate. Perhaps in the field they get trapped by floating debris which may enhance the accumulation of organic material and favour establishment.

According to Bleasdale (1977), tropism is crucial for the determination of plant forms. Possibly, seedlings originating from buoyant seeds lack photo-geotropism, which could explain the warped stalks in inundated seedlings of *S. martiana* and *P. munguba*. However, water originating from várzea rivers is characterized by a high content of nutrients (Furch and Klinge, 1989), which might contribute to a different seedling physiognomy in the natural environment than it was in our experiment, where comparatively nutrient poor tap water had to be used. It is likely that rapid germination and the formation of buoyant seedlings in these species allow establishment with the beginning terrestrial phase.

On theoretical grounds, light transmitted through green leaves underwater tends to promote rather than inhibit germination in contrast to the strong inhibition that occurs

under leaf shade in an aerial environment (Frankland et al., 1987). Whether this has a positive effect on establishment efficiency remains to be tested. In some European herb species no recognizable benefit was found in subhydic germination (Brandes and Evers, 1999). Guillois-Froget et al. (2002) instead found that submerged conditions increased germination but reduced seedling survival in European black willows (*Populus nigra*).

Rapid germination might be an important adaptation of floodplain tree species to the peculiar environmental conditions, favouring establishment during the short terrestrial phase. Oliveira (1998) mentioned that the viability of seeds of *S. martiana* is maximal about 48 h after dispersal. In *Campsandra comosa* Benth., which occurs in Amazonian nutrient poor black-water (igapó) forests, viability of seeds is reported to last for about 24 days (Parolin, 2001), which still can be considered as a short period when compared to seed viabilities in non-flooded tropical forests, which can last to up to several years (Vazquez-Yanes and Orozco-Segovia, 1990).

The efficient establishment and regeneration of floodplain tree species may be enhanced by different strategies adopted by the analyzed species: early germination in a still flooded environment seems to be important for the species analyzed here. Germination in buoyant and submerged seeds varies distinctly between species and genotypes of trees (Morinaga, 1926; Kozłowski, 2002) but nothing is specifically known for Amazonian floodplain trees. Scarano et al. (2003) found that *Carapa guianensis* showed physiological variation regarding dormancy in response to seed flotation: Germination during and

Table 3

Germination rates, significance, and variance between uncovered and hair-embedded seeds of *S. martiana* and *P. munguba* in the treatments W (seeds positioned in tap water for a period of 14 days and afterwards moved to várzea substrate) and S (seeds positioned directly in várzea substrate) after 14 and 84 days

	Treatment	14 days			84 days		
		<i>t</i> -Value	<i>p</i>	<i>F</i> -ratio variance	<i>t</i> -Value	<i>p</i>	<i>F</i> -ratio variance
<i>S. martiana</i>	W	–1.13	0.29	4.57	Ident.	Ident.	Ident.
	S	5.29	0.001	2.49	Ident.	Ident.	Ident.
<i>P. munguba</i>	W	6.53	0.001	1.16	6.53	0.001	1.16
	S	0.15	0.89	2.38	–2.32	0.05	4.01

Each treatment represents 250 (=5 × 50) seeds. Ident. = no changes between 14 and 84 days of treatment.

after flooding was affected by the length of the floating treatment, increasing length of the floating period meaning decreased germination rates.

The role of fibres surrounding the seeds of *S. martiana* and *P. munguba* remains unclear. Fibre-embedded and waterlogged seeds of *S. martiana* showed the highest germination percentages. In *P. munguba*, the fibre-embedded seeds placed directly on substrate showed higher percentages of germination than the fibre-embedded waterlogged seeds. Possibly, the different dispersal strategies reflect the different ecological niches occupied by both species. *S. martiana* is endemic to Amazonian várzea and colonizes highly inundated riverbanks. The potential of sexual and vegetative reproduction is high and regeneration occurs during the whole year (Oliveira, 1998; Parolin et al., 2002b). Consequently, it is likely that seeds are waterlogged during the longest part of the year, and seeds embedded in fruit-fibres might remain buoyant for longer periods than uncovered seeds. This increases the possibility of long-distance dispersal, and might increase stability of in-water germinated seedlings as well.

Ziburski (1991) mentioned that the fibres contribute to the anemochoric dispersal in *P. munguba*. This species occurs with low frequencies also in non-flooded terra firme forests and savannas (Worbes et al., 1992; Wittmann et al., 2004). During the germination experiment of the present study, fibre-embedded seeds showed highest germination percentages when not waterlogged, which would support anemochoric dispersal in *P. munguba*. However, in Amazonian floodplains, the majority of fibre-embedded seeds drop into the water, where they remain buoyant during several hours. Fibres possibly protect the small seeds from the contact with the water surface, and fibres might increase seedling stability when seeds germinate above the water surface and/or at the riverbanks. Although endozoochory is not the primary dispersal mean in Bombacaceae, it is likely that fibre-embedded buoyant seeds of *P. munguba* are better visible at the water surface than fibre-free seeds, which might increase the possibility of predation and dispersal by aquatic dispersers. Thus, *P. munguba* combines several means of dispersal, which shows that it is a generalist species, well adapted to the periodical inundations, but also with successful dispersal in non-flooded environments.

Seeds of many floodplain trees do not germinate in the water but have extremely flooding tolerant seedlings once they have established (Lobo and Joly, 1996; Parolin and Junk, 2002; Koshikene, 2005). Combinations of adaptations regarding seed germination, seedling development, and traits of roots, shoots and leaves result in a variety of growth strategies among trees. These lead to specific species distributions and zonations along the flooding gradient, and within Amazonian floodplain systems with different environmental conditions depending on the quality of the flooding rivers (Parolin et al., 2004).

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References

- Ayres, J.M., 1993. As matas de várzea do Mamirauá. In: Sociedade Civil Mamirauá (Ed.) Estudos de Mamirauá, vol. 1., Brasília, pp. 1–123.
- Bleasdale, J.K.A., 1977. Fisiologia vegetal. São Paulo: EPU/EDUSP, p. 176.
- Brandes, D., Evers, C., 1999. Germination of seeds under water: A strategy only for waterborne alpine and sub alpine plants? Braunsch. Naturkundl. Schr. 5, 947–953.
- Fernandes-Corrêa, A.F., Furch, B., 1992. Investigations on the tolerance of several trees to submergence in blackwater (igapó) and white-water (várzea) inundation forests near Manaus, Central Amazonia. Amazoniana 12, 71–84.
- Fernandez, M.D., Pieters, A., Donoso, C., Herrera, C., Tezara, W., Rengifo, E., Herrera, A., 1999. Seasonal changes in photosynthesis of trees in the flooded forest of the Mapipe River. Tree Physiol. 19, 79–85.
- Ferreira, C.S., 2002. Germinação e adaptações metabólicas e morfo-anatômicas em plântulas de *Himantus sucuba* (Spruce) Wood., da ambientes de várzea e terra firme na Amazônia Central. Msc.-Diss. INPA/FUA, Manaus, Brazil.
- Frankland, B., Bartley, M.R., Spence, D.H.N., 1987. Germination under water. In: Crawford, R.M.M. (Ed.), Plant Life in Aquatic and Amphibious Habitats. Special Publication Series of the British Ecological Society, Number 5. Blackwell Scientific Publications, Oxford, England, pp. 167–178.
- Furch, B., Klinge, H., 1989. Chemical relationships between vegetation, soil and water in contrasting inundation areas of Amazonia. In: Proctor, J. (Ed.), Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Blackwell, Oxford, pp. 189–204.
- Gottsberger, G., 1978. Seed dispersal by fish in inundated regions of Humaitá, (Amazonas). Biotropica 10, 170–183.
- Goulding, M., 1980. The Fishes and the Forest. Exploitations in Amazonian Natural History. University of California Press, Berkeley.
- Goulding, M., 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. Sonderbd. Naturwiss. Ver. Hamburg 7, 271–283.
- Guilloy-Froget, H., Muller, E., Barsoum, N., Hughes, F.M.R., 2002. Dispersal, germination, and survival of *Populus nigra* L. (Salicaceae) in changing hydrologic conditions. Wetlands 22, 478–488.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The Flood pulse concept in river-floodplain systems. In: Dodge, D. (Ed.), Proceedings of the International Large River Symposium, Ottawa. Can Spec Publ Fish Aquat Sci, vol. 106, pp. 110–127.
- Koshikene, D., 2005. Estratégias germinativas de sete espécies florestais de diferentes estágios sucessionais da várzea na Amazônia Central. Unpubl. Master Thesis, 74 pp.
- Kozłowski, T.T., 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. For. Ecol. Manage. 158, 195–221.
- Kozłowski, T.T., Pallardy, S.G., 1997. Growth Control in Woody Plants. Academic Press, San Diego, CA, USA.
- Kubitzki, K., 1985. The dispersal of forest plants. In: Prance, G.T., Lovejoy, T.E. (Eds.), Amazonia-Key Environments. Pergamon, pp. 129–163.
- Kubitzki, K., Ziburski, A., 1994. Seed dispersal in flood plain forest of Amazonia. Biotropica 26, 30–43.
- Lobo, P.C., Joly, C.A., 1996. Ecophysiology of the germination of *Talauma ovata* St. Hil (Magnoliaceae), a typical tree of the swampy forests. Rev. Bras. Bot. 19, 35–40.
- Lopez, O.R., 2001. Seed flotation and postflooding germination in tropical terra firme and seasonally flooded forest species. Funct. Ecol. 15, 763–771.
- Mannheimer, S., Bevilacqua, G., Caramaschi, E.P., Scarano, F.R., 2003. Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. J. Trop. Ecol. 19, 215–218.
- McHargue, L.A., Hartshorn, G.S., 1983. Seed and seedling ecology of *Carapa guianensis*. Turrialba 33, 399–404.

- Miquel, S., 1987. Morphologie fonctionnelle de plantules d'espèces forestières humides d'Afrique. Rapport du Séminaire sous-régional, 1–8 juillet 1985, Makokou, Gabon. UNESCO, Paris.
- Morinaga, T., 1926. Germination of seeds under water. *Am. J. Bot.* 13, 126–140.
- Ng, F.S.P., 1978. Strategies of establishment in Malayan forest trees. In: Tomlinson, P.B., Zimmerman, M. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, New York, USA, pp. 129–162.
- Oliveira, A.C. 1998. Aspectos da dinâmica populacional de *Salix martiana* Leyb. (Salicaceae), em áreas de várzea da Amazônia Central. Msc.-Diss. INPA/FUA, Manaus, Brazil.
- Parolin, P., 2001. Seed germination and early establishment of 12 tree species from nutrient-poor Central Amazonian floodplains. *Aquat. Bot.* 70, 89–103.
- Parolin, P., Junk, W.J., 2002. The effect of submergence on seed germination in trees from Amazonian floodplains. *Boletim Museu Goeldi* 18/2, 321–329.
- Parolin, P., Armbruster, N., Wittmann, F., Ferreira, L.V., Piedade, M.T.F., Junk, W.J., 2002a. A review of tree phenology in Central Amazonian floodplains. *Pesq. Bot.* 52, 195–222.
- Parolin, P., Oliveira, A.C., Piedade, M.T.F., Wittmann, F., Junk, W.J., 2002b. Pioneer trees in Amazonian floodplains: key species form monospecific stands in different habitats. *Fol. Geobot.* 37, 225–238.
- Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Schmidt, W., Piedade, M.T.F., Junk, W.J., 2004. Central Amazon floodplain forests: tree survival in a pulsing system. *Bot. Rev.* 70, 357–380.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon. In: Prance, G., Lovejoy, T. (Eds.), *Key Environments: Amazonia*. Oxford, pp. 109–145.
- Prance, G.T., 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 3, 26–38.
- Scarano, F.R., 1998. A comparison of dispersal, germination and establishment of woody plants subjected to distinct flooding regimes in Brazilian flood-prone forests and estuarine vegetation. In: Scarano, F.R., Franco, A.C. (Eds.), *Ecophysiological Strategies of Xerophytic and Amphibious Plants in the Neotropics*, 4. *Oecol. Bras.*, pp. 176–193.
- Scarano, F.R., Ribeiro, K.T., Moraes, L.F.D., Lima, H.C., 1997. Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. *J. Trop. Ecol.* 14, 793–803.
- Scarano, F.R., Pereira, T.S., Rocas, G., 2003. Seed germination during flotation and seedling growth of *Carapa guianensis*, a tree from flood-prone forests of the Amazon. *Plant Ecol.* 168, 291–296.
- Schlüter, U.B., Furch, B., Joly, C.A., 1993. Physiological and anatomical adaptations by young *Astrocaryum jauari* Mart. (Arecaceae) in periodically inundated biotopes of Central Amazonia. *Biotropica* 25, 384–396.
- Schöngart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V., Worbes, M., 2002. Phenology and stem growth periodicity of tree species in Amazonian floodplain forests. *J. Trop. Ecol.* 18, 581–597.
- Vazquez-Yanes, C., Orozco-Segovia, A., 1990. Seed dormancy in the tropical rain forest. In: Bawa, K.S., Hadley, M. (Eds.), *Reproductive Ecology of Tropical Forest Plants*. UNESCO/Parthenon, Paris/Carnforth, pp. 247–259.
- Waldhoff, D., Junk, W.J., Furch, B., 1998. Responses of three Central Amazonian tree species to drought and flooding under controlled conditions. *Int. J. Ecol. Environ. Sci.* 24, 237–252.
- Wittmann, F., Parolin, P., 1999. Phenology of six tree species from Central Amazonian várzea. *Ecotropica* 5, 51–57.
- Wittmann, F., Parolin, P., 2005. Aboveground roots in Amazonian white-water forests. *Biotropica* 37, 609–619.
- Wittmann, F., Anhof, D., Junk, W.J., 2002. Tree species distribution and community structure of Central Amazonian várzea forests by remote sensing techniques. *J. Trop. Ecol.* 18, 805–820.
- Wittmann, F., Junk, W.J., Piedade, M.T.F., 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Manage.* 196, 199–212.
- Worbes, M., 1986. Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. *Scripta Geobotanica* 17, 1–112.
- Worbes, M., 1997. The forest ecosystem of the floodplains. In: Junk, W. (Ed.), *The Central Amazon Floodplain: Ecology of a Pulsating System*. Ecological Studies, vol. 126. Springer, Berlin, pp. 223–265.
- Worbes, M., Klinge, H., Revilla, J.D., Martius, C., 1992. On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. *J. Veg. Sci.* 3, 553–564.
- Ziburski, A., 1991. Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens. In: Rauh, W. (Ed.), *Tropische und Subtropische Pflanzenwelt*. Akademie der Wissenschaften und der Literatur, 77. pp. 1–96.