

Ecophysiology and morphology of seed germination of the neotropical lowland tree *Genipa americana* (Rubiaceae)

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ABSTRACT. The morphology of *Genipa americana* seeds and post-seminal development was studied, and its germination response investigated in relation to storage in water, substrate water volume, osmotic potential and temperature and light regimes. The seeds are flattened and seedlings are phanerocarpic with leafy cotyledons. Seeds stored in water kept viable for up to 6 mo, but germination and seedling emergence were reduced after 4 mo. Germination was not affected under water-logged conditions, but seedling emergence was reduced at the water volume corresponding to a water column two times deeper than the seeds' mean thickness (70 ml). When seeds were osmotically stressed, a reduction in the rate and germination percentage occurred at -0.2 MPa and germination was drastically inhibited at -0.6 MPa. Seeds germinated in a wide range of temperatures (15–40 °C), with optimum at continuous temperatures of 25 and 30 °C. Light was not required for germination, and no dormancy mechanisms were observed. The seed and seedling morphology and the germinative responses of the species may permit its regeneration in periodically flooded lowland forests and riparian habitats and are probably key factors in explaining the species' wide distribution.

KEYWORDS: ecophysiology, flooding, *Genipa americana*, germination, light, morphology, seed longevity, seedling emergence, temperature, water potential

INTRODUCTION

Wetlands are special places. They cover *c.* 6% of the earth's land surface and are among the most threatened ecosystems (Maltby 1991). They are highly suitable for plant ecological studies due to their spatial and temporal variability

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(Joly 1991, Klinge *et al.* 1990) and to the aquatic–terrestrial gradient they represent (Malanson 1993), promoting the maintenance of dynamic and unpredictable communities (Nilsson *et al.* 1988). In this respect, South America is characterized primarily by large watersheds (Klinge *et al.* 1990), occurring in Brazil as floodplains (the ‘pantanal’ complex and ‘várzea’) and gallery forests (Joly 1991). Many of these riverine ecosystems present intense erosional and depositional activity, playing an important role in forest regeneration and species diversity in the associated forests (Salo & Kalliola 1991). However, germinative strategies of plant species that allow successful regeneration in Brazilian freshwater wetlands are poorly known (Scarano *et al.* 1997) and, with rare exceptions, the first experimental results have only recently been published (e.g. Coutinho & Struffaldi 1971, Lieberg & Joly 1993, Lobo & Joly 1996, Scarano & Crawford 1992, Scarano *et al.* 1997).

A few years ago, reviewing the patterns of seed longevity and germination in the tropics, Vázquez-Yanes & Orozco-Segovia (1993) asserted that knowledge of ecophysiology of seed germination is essential to understanding processes such as plant establishment, succession and natural regeneration, and thus is one of the basic tools for plant population management. On the same occasion, they lamented the scarcity of information on the physiology and ecology of seeds of tropical species and the fact that most of the experimental research done in laboratories lacks meticulous seed handling, simulation of the natural environmental conditions, as well as ecological orientation. Additionally, of the numerous published papers on seed germination and seedling growth and survival, only a handful describe the initial morphology, size, or developmental stage of the seedlings studied, which are essential for understanding ecological processes (Garwood 1996).

In this study the germinative response and seedling emergence of *Genipa americana* L. (Rubiaceae) are examined in relation to some of the main environmental factors (longevity of water-stored seeds, substrate water volume, water stress, light and temperature) to which the seeds of this species are subjected in its habitat, as well as the morphology of seeds and post-seminal development. *Genipa americana*, hereafter referred to as *Genipa*, is a semideciduous tree with a maximum height of *c.* 25 m, known in Brazil as ‘jenipapo’, which occurs in flood-prone forests, including the seasonal swamp forests on waterlogged soils irregularly flooded by small streams during the rainy season, as well as in secondary succession forests subjected to some degree of flooding (Carvalho 1994). It is widely distributed throughout the neotropical forests, ranging from Mexico to northern Argentina, and its edible fruits are commonly used by local populations (FAO 1986), consumed *in natura* or used to make juice or fruit-jelly. Due to its tolerance to flooding and to the fact that its fruits are highly attractive to the fauna, *Genipa* has been used in regeneration models for disturbed riparian environments (Barbosa *et al.* 1992, Carvalho 1994).

METHODS

Seeds were collected from ripe fruits of some adult trees of the Rio de Janeiro Botanical Garden Arboretum (22°58'S; 43°13'W – Rio de Janeiro State) and Brasilia urban Arboretum (15°30'S; 48°17'W – Distrito Federal). Due to the fact that the trees from both places are cultivated, their origin is unknown. The seeds from both localities showed no differences in initial moisture content (60.2%) and germination (98%), and were considered as a single seed pool in the experiments. The experiments were carried out in the Seed Laboratory of the Rio de Janeiro Botanical Garden. To prevent fungal infection, seeds were treated with 10% NaClO for 10 min before being stored at 15 °C in darkness, for periods ranging from 3 to 10 d, without any drying treatment.

Germination tests were performed at 30 °C in transparent plastic boxes ('gerbox') filled with heat-sterilized vermiculite as recommended by Andrade *et al.* (in press), except for the water stress and substrate water volume experiments, where two filter papers wet in distilled water or osmotic solution were used instead of vermiculite. Experiments were carried out in temperature and light controlled chambers, with temperature kept constant within ± 1 °C and, unless light was an intended variable, an 8 h light/16 h darkness regime was used (4×20 W white fluorescent tubes; total flux rate $20 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Measurements were taken three times a week and the number of germinated seeds and emerged seedlings was recorded until neither of the parameters increased anymore. The criterion for germination was visible radicle protrusion. Seedlings with expanded cotyledons and completely developed structures were considered as emerged, except for the water stress experiment, in which seeds with 5 mm-long radicles were considered as emerged seedlings. Seeds showing external signs of rotting and seedlings with rotting signs on the hypocotyl were considered dead. The rate of seed germination was estimated using the index of germination velocity (IGV) (Labouriau 1970): $\text{IGV} = 1/\bar{t} = \sum n_i / \sum n_i \cdot t_i$, where \bar{t} is the average germination time, t_i is the number of days between the beginning of the experiment and the i th observation, and n_i is the number of seeds germinated within the time interval $t_{i-1} - t_i$. Percentage values are means of four replicates. Due to limited seed availability, 25 seeds per replicate were used in all experiments except for the water stress and light regimes ones, in which 40 seeds were used. Vertical lines and \pm values represent 1 SE.

Data were subjected to single or two-factor ANOVA after arcsine transformation, and Tukey's multiple comparison procedure was used to compare significant differences between treatment means (Zar 1996). Whenever the result of a replicate was zero or 100% the relative values of $1/4n$ or $1 - 1/4n$ were used, respectively, to calculate proportions before transformation (n is the number of seeds per replicate; Zar 1996). Throughout, results in which $P < 0.05$ are reported as significant.

Seed and seedling morphology

For seed and post-seminal development descriptions, two sets of 25 seeds were sown in transparent plastic boxes filled with vermiculite, kept on the window-sill under laboratory conditions (25–27 °C ambient temperature and 80% relative humidity), placed in order to receive 2–3 h d⁻¹ of direct sunlight. Descriptive terminology was based on Stearn (1983); seeds and seedlings were drawn with the aid of a camera lucida fitted on a stereomicroscope.

Effect of storage in water

Sets of 120 seeds were stored in transparent glass bottles filled with 250 ml of distilled water at 25 °C. In order to prevent microalgae proliferation, the bottles were covered with black plastic bags. The seed content of one bottle was submitted to a germination test monthly, under the standard conditions previously described.

Effect of substrate water volume

Water volume treatments of 5, 10, 15, 20, 25, 30, 40, 50, 60, 70 and 80 ml were used to submit the substrate to waterlogging regimes ranging from humid to inundated by a water column two and a half times deeper than the seeds mean thickness (80 ml). The water content was renewed weekly; to avoid evaporation losses the plastic boxes were sealed with adhesive tape.

Effect of water stress

Aqueous (distilled water) solutions of mannitol mixed after Salisbury & Ross (1992) were used to exert osmotic potentials (ψ_s) of -0.2, -0.4, -0.6, -0.8, -1.0, -1.2, -1.4 and -1.6 MPa (1 MPa = 10 bars). In order to avoid evaporation losses, the plastic boxes were sealed with adhesive tape. After 2 mo the osmotica were replaced by distilled water in order to examine whether the non-germinated seeds had lost their viability or failed to germinate.

Effect of constant temperature regimes

Seeds were germinated under constant temperatures in 5 °C increments from 15–40 °C.

Effect of light regimes

Light requirement for seed germination was investigated by the comparison of the germinative response in black and transparent plastic boxes. The two light treatments were conducted at 30 °C and 20–30 °C (16/8h thermoperiod) to investigate the interaction of light and temperature. Seed germination and seedling emergence recordings were carried out in a dark room using green safety light.

RESULTS

Morphology of seed and post-seminal development

Fruits are large indehiscent berries (mean fresh weight = 113.5 ± 40.3 g, $n = 48$) with a fleshy, sweet mesocarp, containing 150–500 seeds. Seeds (Figure 1a–d) are flattened; irregularly circular or angular in outline ($8.5 \pm 0.1 \times 6.5 \pm 0.1 \times 2.1 \pm 0.03$ mm, $n = 100$; mean fresh wt. = 0.096 ± 0.001 g, $n = 99$), slightly elliptic in transversal section, with faces slightly convex and round borders; base acuminate. The seed coat is thin (<1 mm), with the outer surface opaque, yellowish (ripe seed) and slightly wrinkled; seminal stigmas not perceptible. While humid, the seeds are covered with a thin endocarpic mucilaginous tissue; in dry seed, the whitish mucilage adheres to the seed surface as a membrane. The endosperm is horny and the embryo, spatulate: embryonic axis circular in transversal section and not concealed by the ovate cotyledons. The flotation of seeds (tested using five replicates of 20 seeds in distilled water) was 0%, while 90% of 15 mature fruits floated in distilled water.

Morphologically, germination (Figure 1e–g) begins through radicle protrusion (8–13 d after sowing), and the hypocotyl differentiation closely follows radicle emergence. Cotyledons fully escape seed and emerge around 27–34 d (Figure 1i), after a period of hypocotyl growth and secondary roots differentiation (Figure 1h). Seedlings (Figure 1j) are phaneroepigeal (*sensu* Duke & Polhill 1981), with thick taproot, tapering, sinuous, with many whitish-brown secondary roots and conspicuous collet (Figure 1k), with adventitious roots. The hypocotyl (3.7 ± 0.1 cm long; $n = 30$) is circular in transversal section, glabrous and green; the plumule is reduced and cotyledons (Figure 1l) are short-petiolate, blades are oblong, glabrous above and below, membranous and with a mid-vein conspicuous and slightly raised below, and persistent for as long as 1 y under laboratory conditions. First leaves (Figure 1l) spread open from 77 to 96 d, and are lanceolate, with the apex and base acute, have integer margins, and are green, distichous on the trunk. The general appearance of the first leaves is similar to that of older ones.

Effect of storage in water

When transferred from bottles to germination boxes with low water content filter paper (10 ml), the germination was high ($>80\%$) for the first 4 mo of storage, but showed significant decreases both at 5 and 6 mo, and ceased completely from the 7th month (Figure 2) (ANOVA $F = 136.6$; $df = 8, 27$; $P < 0.0001$). The reduction in the number of germinating seeds was accompanied by an increase in the number of dead seeds. It is interesting to note that, although the proportion of rotten seeds increased with time of submergence, seedling emergence remained close to the corresponding germination values, showing that the surviving proportion of the seed population did not suffer any serious injury to its inner structures, and was able to produce normal seedlings. No germination took place under water inside the glass bottles.

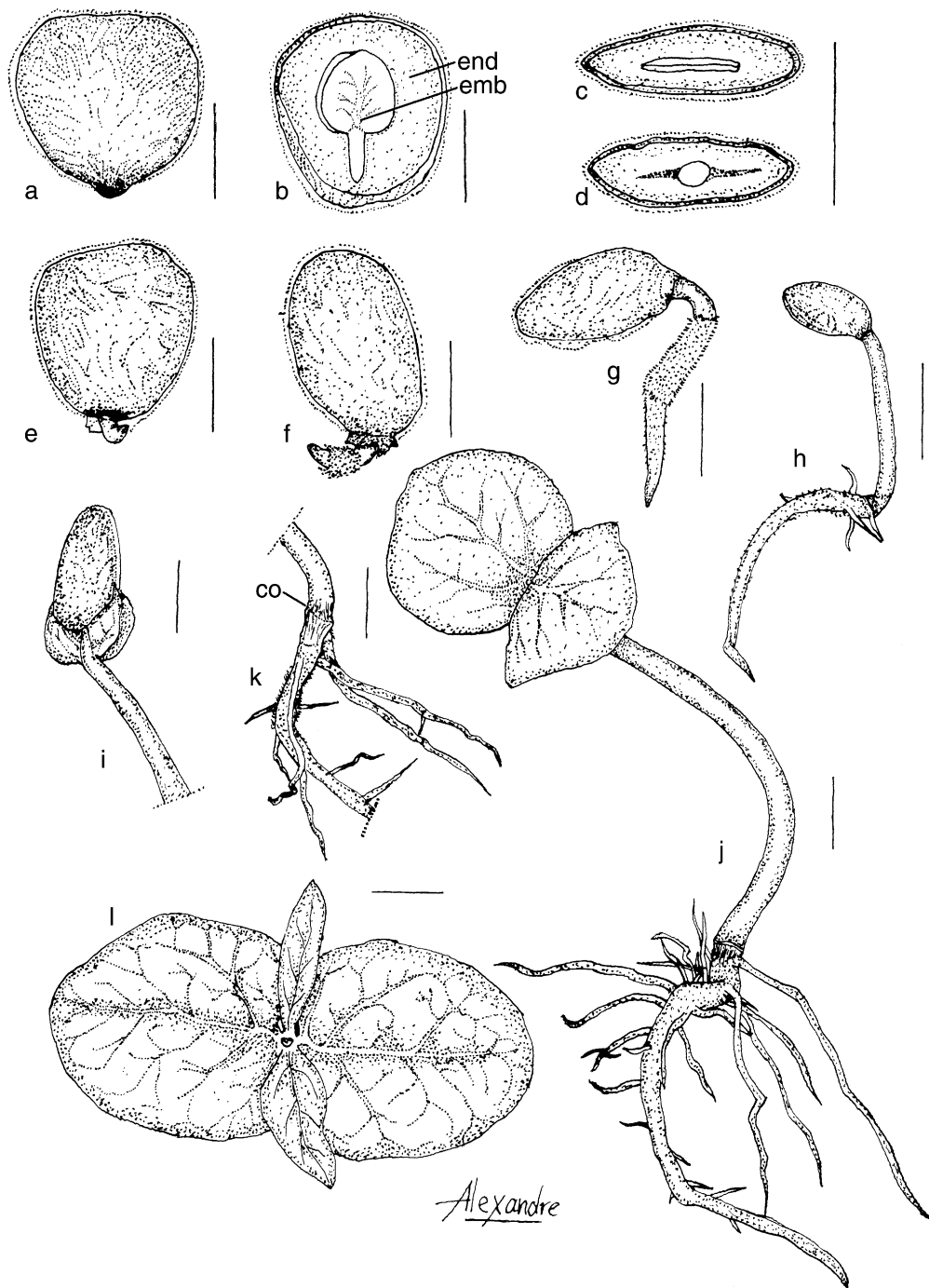


Figure 1. Morphology of seed and post-seminal development of *Genipa americana*. Seed: (a) external view; (b) longitudinal section showing endosperm (end) and embryo (emb) in outline; (c) transversal section showing juxtaposed cotyledons; (d) transversal section showing embryonic axis. Germinating seed: (e) radicle protrusion; (f) and (g) hypocotyl differentiation; (h) enclosed cotyledons lifted above the ground by hypocotyl; (i) emerging cotyledons. Seedling: (j) general appearance; (k) secondary roots and collet (co); (l) cotyledons and first leaves. Scale bars: 5 mm.

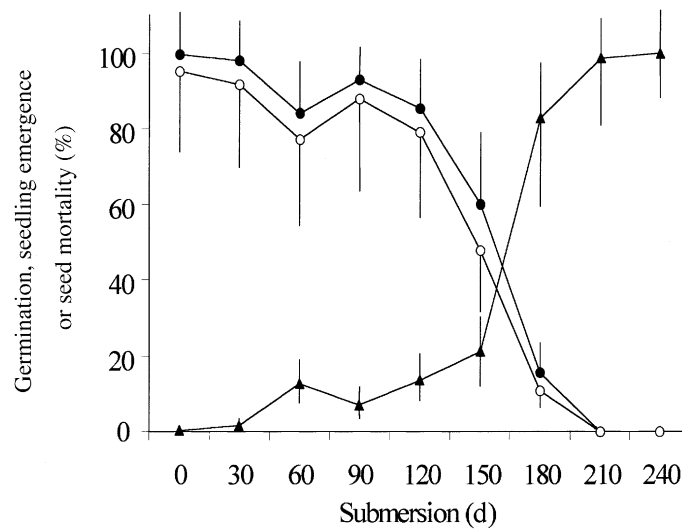


Figure 2. Effect of storage in water for different time periods on seed germination (●), seedling emergence (○) and seed mortality (▲) of *Genipa americana*.

Effect of substrate water volume

Seed germination was not affected by the increase of the substrate water content, but at the higher volume (80 ml) a significant decrease in germination rate indicated that seed vigour was affected at this level ($F = 35.2$; $df = 10, 33$; $P < 0.0001$) (Figure 3). Indeed, seedling emergence was shown to be more sensitive to the water regime, being significantly reduced at 80 ml ($F = 7.1$; $df = 10, 33$; $P < 0.0001$) and markedly reduced at 70 ml. Thus, the seeds were

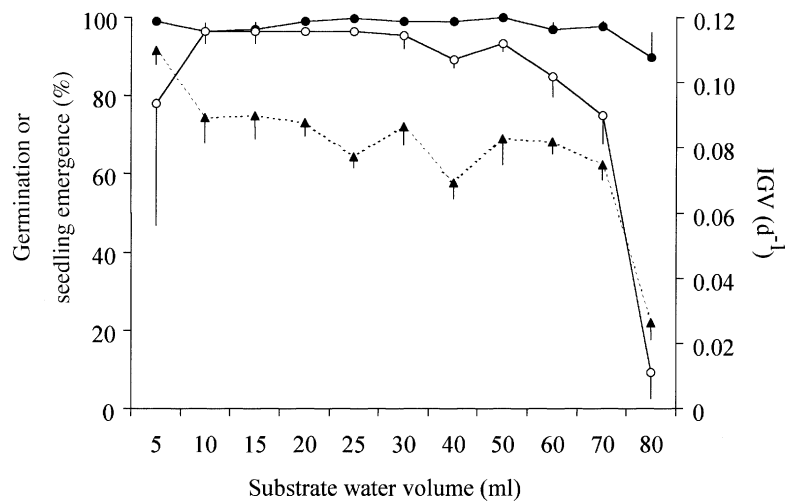


Figure 3. Effect of progressive levels of substrate water volume on per cent germination (●), germination rate (IGV) (-▲-) and seedling emergence (○) of *Genipa americana*.

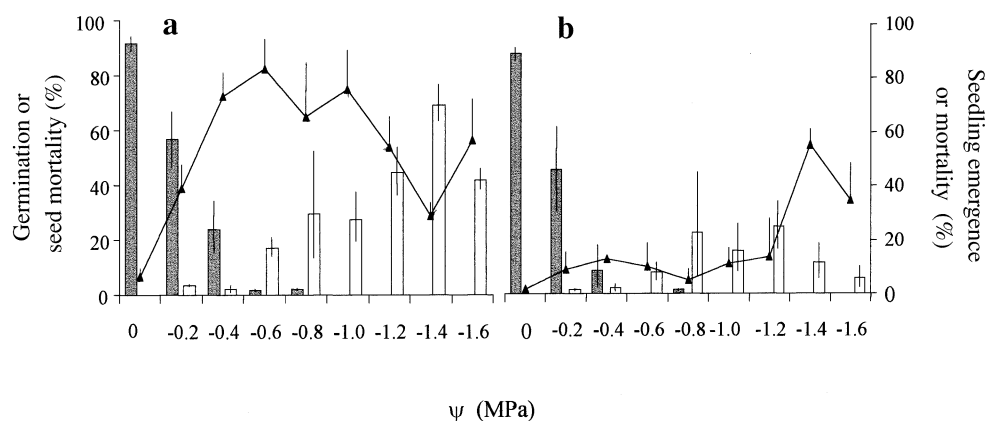


Figure 4. Seed (a) and seedling (b) responses of *Genipa americana* to water stress. In each graph, filled bars represent germination or seedling emergence and (line, \blacktriangle) represents mortality under mannitol solutions, while open bars are germination or seedling emergence after substitution of different osmotica by distilled water.

able to germinate and produce seedlings when submerged by a water column two times deeper than the seeds, mean thickness (70 ml).

Effect of water stress

Seeds were very sensitive to an external osmotic stress, as shown by a large decrease in germination percentage as a result of the lowering of the external water potential (Figure 4). Germination ($F = 65.8$; $df = 8, 27$; $P < 0.0001$) and seedling emergence ($F = 31.0$; $df = 8, 27$; $P < 0.0001$) were significantly reduced at -0.2 and -0.4 MPa and completely inhibited at -1.0 MPa. Also, as expected, the lower the ψ_s , the slower the germination (data not shown). Almost all non-germinated seeds at -0.2 and -0.4 MPa died, and seed mortality for intermediate osmotica (from -0.4 to -1.0 Mpa) was significantly higher than the other treatments ($F = 3.9$; $df = 8, 27$; $P = 0.0041$) (Figure 4a). Seeds submitted to the lower osmotic potentials were covered by much more mucilage than normal.

Seed mortality would likely keep on increasing if the exposure time to simulated drought was lengthened; however, almost all seeds which did not germinate or die under water stress germinated when the mannitol solutions were replaced by distilled water (Figure 4a), attaining higher values at the three lower potentials ($F = 8.7$, $P < 0.0001$). This result suggests that *Genipa* seeds fail to germinate (are quiescent) under osmotica < -0.6 MPa. Yet, despite the survival of almost all seeds under these osmotica, many of those exposed to the lower potentials failed to generate normal seedlings, and the final seedling emergence was similar in all treatments but control ($F = 9.3$, $P < 0.0001$) (Figure 4b), suggesting that these seeds suffered internal injuries at potentials lower than -1.2 MPa.

Effect of constant temperature regimes

Germination was higher between 20 and 35 °C ($F = 26.5$; $df = 5, 18$; $P < 0.0001$) (Figure 5), showing significant reductions at 15 and 40 °C, and at

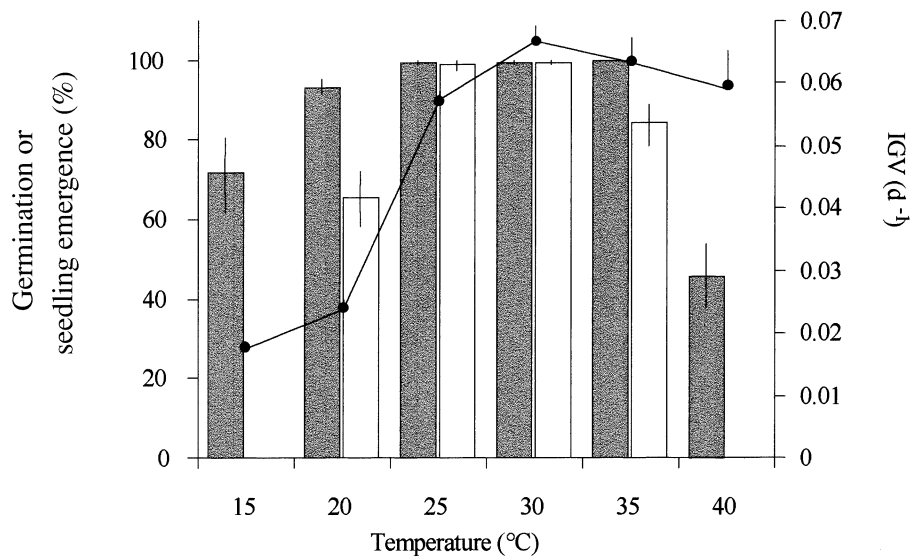


Figure 5. Effect of constant temperatures on per cent germination (filled bars), germination rate (line, —●—) and seedling emergence (open bars) of *Genipa americana*.

this last temperature all non-germinated seeds died and degenerated. Germination rate, unlike percentage values, showed a sigmoid distribution and was retarded at the two lower temperatures ($F = 42.25$; $df = 5, 18$; $P < 0.0001$), with maximum at 30 °C. Seedling emergence followed the same distribution found for germination, but with a shorter range: values significantly higher at 25 and 30 °C and absence of cotyledon expansion at both extreme temperatures, due to seedling suppression at 15 °C and deterioration at 40 °C ($F = 184.6$; $df = 5, 18$; $P < 0.0001$).

Effect of light regimes

Continuous darkness and photoperiod had no effect on germination (Table 1), and the seeds may be regarded as photoblastic neutral. However, germination was slower in the alternating temperature, with a small but significant interaction effect with the light regime (Table 1).

Table 1. Germination percentage and germination rate (IGV) of *Genipa americana* seeds under contrasting temperature (constant v. fluctuating) and light regimes. Only means accompanied by different letters (upper-case for columns, lower-case for lines) differ significantly.

Temperature (°C)	Light		Darkness	
	Germination (%)	IGV (d ⁻¹)	Germination (%)	IGV (d ⁻¹)
30	93.4 ± 0.8 ns	0.08 ± 0.01 Aa	95.8 ± 0.1 ns	0.07 ± 0.01 Ab
20–30	91.1 ± 0.2 ns	0.04 ± 0.00 Ba	95.2 ± 0.1 ns	0.05 ± 0.00 Ba

Light: $F = 0.09$ n.s. ($df = 1, 12$), Temperature: $F = 173.8$, $P < 0.0001$ ($df = 1, 12$); Light × Temp.: $F = 8.9$, $P = 0.0195$ ($df = 1, 12$); ns = not significant ($P > 0.05$).

DISCUSSION

Judging by the present distribution of *Genipa* in the neotropics (Carvalho 1994, Rizzini 1978), it appears probable that its centre of evolution was in Amazonia (Cavalcante 1996). In that region, fluctuations in the water level of the Amazon River and its large tributaries periodically flood extensive areas of tropical rain forest (the 'várzeas') for at least 6 mo y^{-1} (Ayres 1993, Klinge *et al.* 1990). A striking trait of these inundated forests is the synchronization of fruiting and seed dispersal of their tree species during the high water phase (Ayres 1993, Kubitzki & Ziburski 1994).

According to Crestana *et al.* (1992), *Genipa* fruit maturation lasts 12 mo, and throughout most of this time the fruits are able to float if detached from the tree. The end of the maturation period takes place in the beginning of the rainy season, and changes in fruit density provoke its submergence, in a seemingly hydrochoric cycle (Kageyama *et al.* 1989). Nevertheless, *Genipa* seed dispersal is a multiple process, being not only hydrochoric, but also zoochoric: the fruits are taken by fish (Gottsberger 1978), mammals (Chapman 1989, Foster *et al.* 1986, Foster & Janson 1985) and large birds (Foster *et al.* 1986). Finally, despite fruit consumption by frugivorous vertebrates, in the absence of flooding most fruits fall within a few metres of the parent tree (Crestana 1993).

A characteristic shared by the different inundated forests in which *Genipa* occurs (Joly 1991, Junk 1989, Scarano *et al.* 1997) is a high degree of patchiness due to variations in topography, which leads to a flood level gradient from permanently aquatic to permanently terrestrial habitats. It follows that the seed dispersal process may carry the seeds to sites ranging from inundated to dry, the later represented by elevated patches as mounds or fallen trunks (Becker *et al.* 1988), or even by areas not prone to overflow.

In the Amazonian floodplains context, the seeds ultimately sink to the bottom of the inundated forests (Kubitzki & Ziburski 1994), where they must remain quiescent until the end of the flood season. Along the level of flood gradient where *Genipa* is found (Junk 1989), this period lasts for an average 140 d, extending up to 8 mo in exceptionally rainy years (Junk 1989). This picture fits well the longevity of submerged seeds estimated in the present work, which might allow the formation of an ephemeral, submerged seed bank, ensuring seed survival until the retreat of the flood. This strategy is frequently found in species occurring on flood-prone areas (Coutinho & Struffaldi 1971, Kozlowski 1984, Kubitzki & Ziburski 1994, Scarano & Crawford 1992, Scarano *et al.* 1997), and could be an alternative to the formation of 'floating seed banks', observed in species with seeds that float (e.g. Marques 1994, Steege 1994).

In the sequence of events, the short duration of the vegetation period between the floods and the competitive advantages of early germinants (Jones *et al.* 1994) suggest that germinating shortly after the end of the submersion period is vital to the success of a hydrochorous regeneration strategy. Indeed,

Ayres (1993) found that in a central Amazonian floodplain forest the seedlings emerged just after the rainfall peak, as soon as the soils reappeared. Thus, the ability of *Genipa* seeds to germinate underwater in response to rises in the oxygen concentration provoked by the reduction of the water-line may be of competitive significance. At this phase of the establishment process, dark germination could be important for those seeds buried in the top few mm of the soil, since physiologically and ecologically significant amounts of light rarely penetrate more than 4–5 mm through soil (Vázquez-Yanes *et al.* 1990).

As emphasized before, the pattern of seedfall across the landscape may lead the seeds to patches where water is not readily available, and the results of the water stress experiment suggests that *Genipa* establishment may be hampered under such conditions. Compared to species adapted to dry habitats (Cordero & Molano-Flores 1997, Everitt 1983, Thanos & Skordilis 1987), the osmotic potential in which the germination is inhibited is extremely high (less negative). Under these circumstances, the quiescence of the seeds at the lower potentials may function as a protective mechanism, limiting germination to adequate water availability conditions for germination and seedling development (Vleeshouwers *et al.* 1995), and represent a phase of the habitat choice process imposed on the species by its environment (Schupp 1995). Furthermore, the fact that just a part of the seed population displayed such quiescence might be of adaptive value, representing a trait particularly susceptible to selection pressures exerted by drier sites or patches under unstable water regimes.

Considering that in the Amazonian main river floodplains the periodic inundations frequently cover wide areas of closed forest, depositing casually the diaspores of many species in the understorey (Ayres 1993, Foster *et al.* 1986), a germinating seed must face the hazards related to water under the microclimatic conditions prevailing on the forest floor. Indeed, adaptations to establishment in such mature forest habitats, where temperature and humidity regimes are not subject to remarkable fluctuations (Crawford 1989), include having the optimal percentage and germination rate around 30 °C (Vázquez-Yanes & Orozco-Segovia 1984) and the absence of thermoperiod-regulated germination (Vázquez-Yanes & Orozco-Segovia 1993), as reported here for *Genipa*. Thus, *Genipa* germinative response in relation to temperature and light conforms to the definition of small gap species (*sensu* Denslow 1987) or climax species (*sensu* Swaine & Whitmore 1988) syndromes, which may germinate in the understorey but depend on small canopy openings for substantive growth and reproduction. The recognition of this regenerative strategy is confirmed by the high humidity content and short viability of the seeds under conventional storage conditions (*c.* 6 mo; A. C. S. Andrade, unpubl. data), which imply high oxygen consumption rates, characteristic of shade-tolerant species (Garwood & Lighton 1990).

Further, *Genipa* seedlings are relatively big and considerably slow growing

(Barbosa *et al.* 1992), bear long-lasting green cotyledons and may grow under low level waterlogged conditions for at least 4 mo (Andrade *et al.* in press). Thus, seed-seedling conflicts, as discussed by Schupp (1995), are unlikely to occur for this species, and the probabilities of survival at the seed and seedling stages are likely concordant for a given patch, a finding also true for other species typical of flood-regulated habitats, both in the Amazon and the south-eastern forests (Coutinho & Struffaldi 1971, Lieberg & Joly 1993, Marques 1994, Steege 1994). Additionally, the picture of *Genipa* as a species in which germination is flood-regulated and which is mostly found as an adult in light-gaps (Foster & Janson 1985) corroborates the recent hypothesis that flooding, interacting with light availability, can determine spatial patterns of tree regeneration by causing differential germination or survival among seedlings (e.g. Jones *et al.* 1994, Hall & Harcombe 1998).

Finally, it could be argued that *Genipa* has evolved a number of germinative features that, combined with the variety of dispersal traits it also presents, not only allows colonization of flood-prone habitats, but has also promoted its diffusion (*sensu* Malanson 1993) through riparian landscapes. This movement probably took place across the dendritic net of gallery forests, extending in a northwest–southeast direction to connect the Amazonian and Atlantic forests as well as through the northeastern semi-arid Caatinga via the ‘brejo’ forests (Oliveira-Filho & Ratter 1995). This route of expansion has been recognized as an important one for a number of species during the Pleistocene (Oliveira-Filho & Ratter 1995, Whitmore & Prance 1987), and it should be considered that the invasion of the Atlantic forests by *Genipa* may have occurred for long enough to permit the speciation of *G. infundibuliformis* Zappi & Semir, endemic to the southeast (Zappi *et al.* 1995). As a final remark, it must be added that the intensive utilization of *G. americana* by the Indians since ancient times (Cavalcante 1996, Corrêa 1978) may also have favoured its wide distribution in the neotropics.

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