

Cyrille CORNU^{1, 2}
Wilfried RAMAHAFALY²
Pascal DANTHU^{3, 2}

¹ Cirad
Umr Tetis
Campus international de Baillarguet
34398 Montpellier Cedex 5
France

² Cirad
DP Forêts et Biodiversité
BP 853, Antananarivo
Madagascar

³ Cirad
Ur Bsef
Campus international de Baillarguet
34398 Montpellier Cedex 5
France

Adansonia madagascariensis, a marine hydrochory hypothesis



Photo 1.

Adansonia madagascariensis is often found in thalwegs, bordering temporary and permanent water courses and by the sea, at the edge of tidal zones. In this photo, a mature fruiting baobab by the sea in the bay of Diego-Suarez.

Photo C. Cornu.

RÉSUMÉ

ADANSONIA MADAGASCARIENSIS, UNE HYPOTHÈSE D'HYDROCHORIE MARINE

Des fruits d'*Adansonia madagascariensis* ont été trouvés en mai 2011 sur la plage d'Anjiabe au Nord de Madagascar. Les traces présentes sur les fruits et l'absence de peuplements de l'espèce sur cette côte indiquent qu'ils ont séjourné longtemps en mer. La viabilité des graines contenues a été évaluée et comparée à celle de graines collectées sous des semenciers. Les résultats montrent que leur potentiel germinatif n'est pas altéré par un séjour en mer et que leur germination est possible, voire favorisée dans les zones tidales. Ces premiers résultats confirment l'hypothèse d'une hydrochorie maritime pour cette espèce. Ils montrent que les fruits de baobab peuvent séjourner en mer et conserver des graines viables pour coloniser de nouveaux espaces. Ils pourraient ainsi expliquer la fréquente présence de cette espèce le long du littoral malgache et celle, bien que plus rare, sur les côtes mahoraises.

Mots-clés : *Adansonia madagascariensis*, baobabs, fruits, hydrochorie marine, graines, germination, biogéographie, Madagascar.

ABSTRACT

ADANSONIA MADAGASCARIENSIS, A MARINE HYDROCHORY HYPOTHESIS

Adansonia madagascariensis fruits were found in May 2011 on the beach of Anjiabe in the north of Madagascar. Marks found on the fruits and the absence of this species on this coast indicated that the fruits had been in the sea for a long time. The viability of seeds contained in these fruits was assessed and compared to the viability of seeds collected from under trees. The results show that the time spent in the sea did not affect their germination potential and that germination is possible, and even improves, in tidal zones. These initial results confirm the hypothesis of marine hydrochory for this species. They show that baobab fruits can remain in the sea without affecting the viability of seeds to colonize new areas. This could explain the frequent occurrence of this species along the coast of Madagascar and, more rarely, on the Mayotte coast.

Keywords: *Adansonia madagascariensis*, baobabs, fruits, marine hydrochory, seeds, germination, biogeography, Madagascar.

RESUMEN

ADANSONIA MADAGASCARIENSIS, UNA HIPÓTESIS DE HIDROCORIA MARINA

En mayo de 2011 se encontraron frutos de *Adansonia madagascariensis* en la playa de Anjiabe en el norte de Madagascar. Las marcas presentes en los frutos y la ausencia de rodales de la especie en esta costa indican que éstos permanecieron mucho tiempo en el mar. Se evaluó la viabilidad de las semillas de estos frutos y se comparó con la de las semillas recolectadas en portagranos. Los resultados muestran que su potencial germinativo no se ve afectado por el tiempo pasado en el mar y que su germinación no sólo es posible, sino que incluso se ve mejorada en las zonas intermareales. Estos primeros resultados confirman la hipótesis de hidrocoria marina de esta especie y muestran que los frutos de baobab pueden permanecer en el mar manteniendo semillas viables para colonizar nuevos espacios. Esto podría explicar la frecuente presencia de esta especie a lo largo del litoral de Madagascar y, de forma más escasa, en las costas de Mayotte.

Palabras clave: *Adansonia madagascariensis*, baobabs, frutos, hidrocoria marina, semillas, germinación, biogeografía, Madagascar.

Introduction

Madagascar is a biodiversity hotspot (MYERS *et al.*, 2000). The fauna and flora present on the island is unique throughout the world and around 83% of its plant and land vertebrates are endemic (GOODMAN & BENSTEAD, 2005). This uniqueness can be explained partially by the past isolation of the island, as well as the ecological diversity of its natural environments (WILMÉ *et al.*, 2006). Yet this biodiversity is threatened by human activity, both directly (deforestation, slash and burn agriculture) and indirectly (climate change) (GADE, 1996; TANDROSS *et al.*, 2008).

Baobabs feature amongst the emblematic species of Madagascar (WICKENS & LOWE, 2008; PETIGNAT & JASPER, 2012). Of the nine species currently known in the world (BAUM, 1995; PETTIGREW *et al.*, 2012), six are endemic to Madagascar. Three (*Adansonia suarezensis*, *A. perrieri*, *A. grandidieri*) are on the IUCN Red List of Endangered Species (2012), whilst the other three, *A. madagascariensis*, *A. za* and *A. rubrostipa* appear for the moment to be under less threat.

Preservation of this heritage relies on improving knowledge of the biological mechanisms of the species concerned. And yet questions remain regarding modes of dispersal and germination. Previous studies have shown that baobab seeds are adapted to arid climates and to dispersal by zoochory¹, and more specifically, that they have hard seed coats which require extensive scarification to remove the obstacle of seed coat inhibition for germination to occur (BAUM, 1995; ANDRIANTSARALAZA *et al.*, 2010; RAZANAMEHARIZAKA *et al.*, 2006). In historic times, seed dispersal was probably performed by large vertebrates such as giant tortoises (*Dipsochelys* sp.) (ANDRIANTSARALAZA *et al.*, 2013), or even elephant birds (*Aepyornis* sp.), extinct in Madagascar for many centuries (GRANDIDIER, 1905; BAUM, 1996; ANDRIANTSARALAZA *et al.*, 2010; PEDRONO *et al.*, 2013).

Whilst this syndrome of dispersal by zoochory applies to *A. madagascariensis*, a number of observations relating to this species indicate a possible dispersal by hydrochory, dispersal by water. The species, present across a band covering the north-west of the island (figure 1), is in fact often present in the thalwegs and bordering temporary or permanent water courses. It is equally often found close to the sea, at the edge of tidal zones (BAUM, 1995) (photo 1). In the same way as *A. suarezensis* and *A. rubrostipa*, *A. madagascariensis* can be found along the coast where sea water flooding occasionally occurs (BAUM, 1996). Hydrochorous dispersal along rivers or during flooding in the rainy season is a likely occurrence in species with a hard pericarp (*A. digitata*, *A. madagascariensis*, *A. za* and *A. perrieri*) (BAUM, 1996). And finally, *A. madagascariensis* is also not completely endemic to Madagascar as some individual specimens, which appear not to have been transported by man, can be found along the shores of Mayotte (figure 1) (CHARPENTIER, 2006) at Dapani (photo 2a) and Mliha (photo 2b).

The aim of this article is to provide some elements towards testing the hypothesis of a marine hydrochory for *A. madagascariensis*, attempting to distinguish factors associated with fruit dispersal, seed physiology and the environmental context of seeds washed up on the shore.

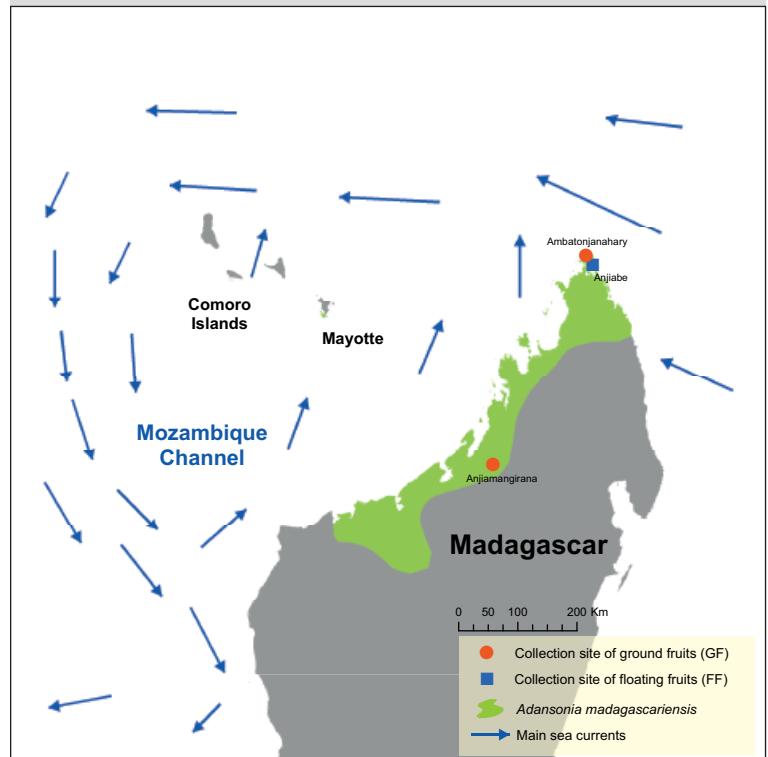


Figure 1.

Area of presence of *A. madagascariensis*, collection site of fruits and surface circulation scheme of water in the Mozambique Channel from DONGUY and PITON (1991).



Photo 2.

Adansonia madagascariensis on the beaches at Mliha (a) and Dapani (b) in Mayotte. Photos J.-P. Lumaret & P. Danthu.

¹ The dispersal of seeds, spores, or fruit by animals.



Photo 3.
Fruit washed up on the beach at Anjiabe.
Photo C. Cornu.



Photo 4.
Fruits and seeds from *Adansonia madagascariensis*:
(a) outer aspect of ground fruit; (b) outer aspect of floating
fruit; (c) inner aspect of ground fruit; (d) inner aspect of
floating fruit.
Photos C. Cornu.

Materials and methods

Our study initially assessed the germination capacity of seeds from fruits that had spent a long time at sea. These fruits are referred to hereafter as “floating fruits” or FF. The results were then compared with the germination capacity of seeds obtained from fruits collected under trees in natural populations (“ground fruits” or GF). The study subsequently assesses the influence of the environmental context and, in particular, of the salt content of substrate on the germination of seeds obtained from fruit washed-up on the shore.

Twenty-nine fruits were picked off the shore in June 2011 from the beach at Anjiabe to the northeast of the town of Diego-Suarez (figure 1). The fruits were found on the foreshore amongst a large amount of other detritus (driftwood, shells, fruit, plastic waste), indicating that they’d been washed-up during a particularly low-tide. Biometric analysis of the fruits and seeds was carried out to identify the species to which the fruits belong.

Similarly, thirty fruits were collected under *A. madagascariensis* in Anjamangirana and Ambatanjanahary, two geographically distant populations with contrasting ecological contexts (figure 1).

The fruits were measured (weight, volume, length). Their external appearance (wear and tear, cracks) and their internal condition (state of seeds, fibres and pulp) (photo 4) has been described. The seeds were then extracted and counted. They were separated from the surrounding pulp, cleaned, measured (photo 5) and weighed. Their viability was visually assessed and mechanically tested using finger pressure. Damaged seeds were discarded. The intact ones were stored in a dry place at an ambient temperature between 15-25°C until they were used in November 2012.

Germination tests were carried out according to the protocol described by RAZANAMEHARIZAKA *et al.* (2006), in plastic germination boxes (17cm x 11cm x 5cm), in the dark, at a temperature of $30 \pm 2^\circ\text{C}$, in a closed atmosphere, on a bed of sand, sterilised and moistened with distilled water. A seed was considered to have germinated when the radicle had emerged from the seed coat. On completion of the experiment, the viability of ungerminated seeds was assessed by dissection.

Two distinct tests were performed. The aim of the first was to evaluate the germination capacity, as defined by CÔME (1968), of seeds that had spent time in the sea compared with seeds from the fruit collected under the trees. Germination capacity is the percentage of seeds able to germinate over a given period under defined conditions. This involved scarifying all the seeds with a treatment of concentrated sulphuric acid (95%) for six hours according to RAZANAMEHARIZAKA *et al.* (2006) to remove their seed coat inhibition. Four repetitions were carried out using ten seeds extracted from six fruits (three each from the sea and the ground).

The aim of the second experiment was to assess the influence of environmental factors, in particular, the salinity of the germination substrate, on the germination capacity of seeds. Three germination substrates were collected *in situ*: (i) from the beach at Anjiabe; (ii) bordering the tidal zone (upper tidal limit); (iii) twenty-five metres beyond that limit.

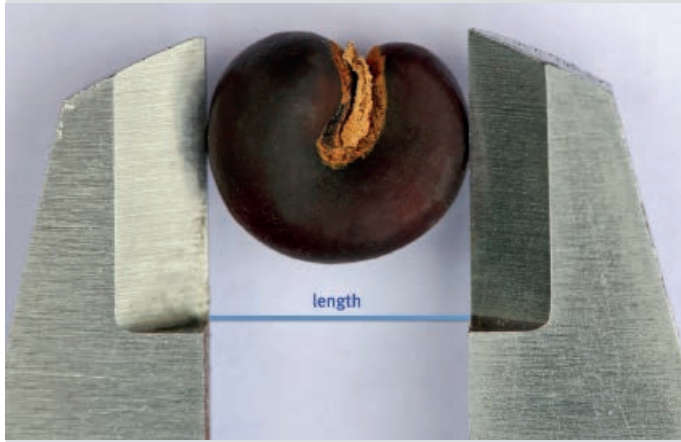


Photo 5.
Reniform seed from *Adansonia madagascariensis*.
Photo C. Cornu.

The control substrate consisted of river sand (collected from the banks of the Ikopa at Antananarivo). The sodium chloride content (expressed in equivalent g-NaCl per kg soil) of the four germination substrates was measured by electrical conductivity. It was 6.40g/kg for the beach sand, 3.43 for the sample collected on the upper limit of the tidal zone, 0.63 for the sample collected 25 metres beyond and 0.13 for the control sand sample. Six fruits were used for this experiment, three FF and three GF. The germination capacity, as defined by CÔME (1968), of forty seeds from each fruit was tested on each type of substrate. Germination rates were checked daily.

The two experiments were considered completed when no new germinations were recorded for three consecutive days. The experiments were completed in twelve days.

The confidence intervals for each mean were calculated at a threshold of 5%. Student's *t*-tests were performed to compare paired means (at a threshold of 5%). A series of χ^2 tests at a threshold of 5% were carried out on the proportions to test the independence of the different classification criteria.

Results

Species identification by biometric analysis of fruits

In the absence of formal taxonomic identification data for the floating fruits, a comparative biometric analysis of the fruits and seeds from the FF was undertaken. Table I shows that the biometric values, length and width of fruits, size and weight of seeds collected from Anjiabe were significantly different to those known for the two other baobab species in the north of Madagascar (*A. suarezensis* and *A. perrieri*). However, they are clearly roughly the same size as those reported in the literature (BAUM, 1995; RAZANAMEHARIZAKA *et al.*, 2006), as well as those measured from the ground fruits of *A. madagascariensis* collected at Ambatonjanahary and Anjiamangirana (CT). Therefore, it can be concluded that the fruits collected on the beach at Anjiabe (FF) belong to the *A. madagascariensis* species.

Effects on the fruits of time spent in the sea..

The outer part of the epicarp of the baobab fruit has a velvety layer (photo 4a). Whilst this layer was absent from 27% of the FF, in the others it was still scantily present and had deteriorated severely (photo 4b). This damage to the epicarp of the fruits is one of the directly noticeable consequences of their prolonged period at sea.

Another noticeable effect was the presence of cracks in 80% of the fruits with only 20% remaining intact. However, on opening, all the fruits were devoid of pulp, with a very small amount of fibre and the frequent presence of sand, indicating that sea water had entered the fruits (photo 4d). The average volume of fruits ranged from $0.42 \pm 0.03\text{g/cm}^3$ at Anjiamangirana and only 0.27 ± 0.02 at Anjiabe, confirming a loss of volume of FF in relation to GF. The sea water which had entered the FF had most likely dissolved all or part of the pulp and destroyed a large majority of the fibres.

Table I.

Comparative biometric values of floating fruits and seeds collected from the beach at Anjiabe with the biometric reference data for *Adansonia suarezensis*, *A. perrieri* and *A. madagascariensis* from BAUM (1995) for fruits (¹ in the table) and from RAZANAMEHARIZAKA *et al.* (2006) for seeds (² in the table), and the measurements collated from the two control lots sampled at Ambatonjanahary and Anjiamangirana.

	Fruits		Seeds	
	Length (cm)	Width (cm)	Length (mm)	Volume (mg)
Floating fruits Anjiabe	6.7 ± 0.7	7.5 ± 0.6	11.4 ± 0.3	410 ± 30
<i>Adansonia suarezensis</i>	20 - 40 ¹	8 - 14 ¹	16.5 ± 0.5 ²	1717 ± 48 ²
<i>Adansonia perrieri</i>	15 - 25 ¹	8 - 13 ¹	12.9 ± 0.2 ²	710 ± 6 ²
<i>Adansonia madagascariensis</i>	≤ 10 ¹	- ¹	10.9 ± 0.4 ²	366 ± 9 ²
<i>Adansonia madagascariensis</i> Ambatonjanahary	7.9 ± 0.9	6.8 ± 0.4	11.5 ± 0.2	350 ± 30
<i>Adansonia madagascariensis</i> Anjiamangirana	6.2 ± 0.4	7.9 ± 0.4	9.5 ± 0.2	210 ± 20



Photo 6.
Seedlings of *A. madagascariensis* from seeds of washed up fruits.
Photo C. Cornu.

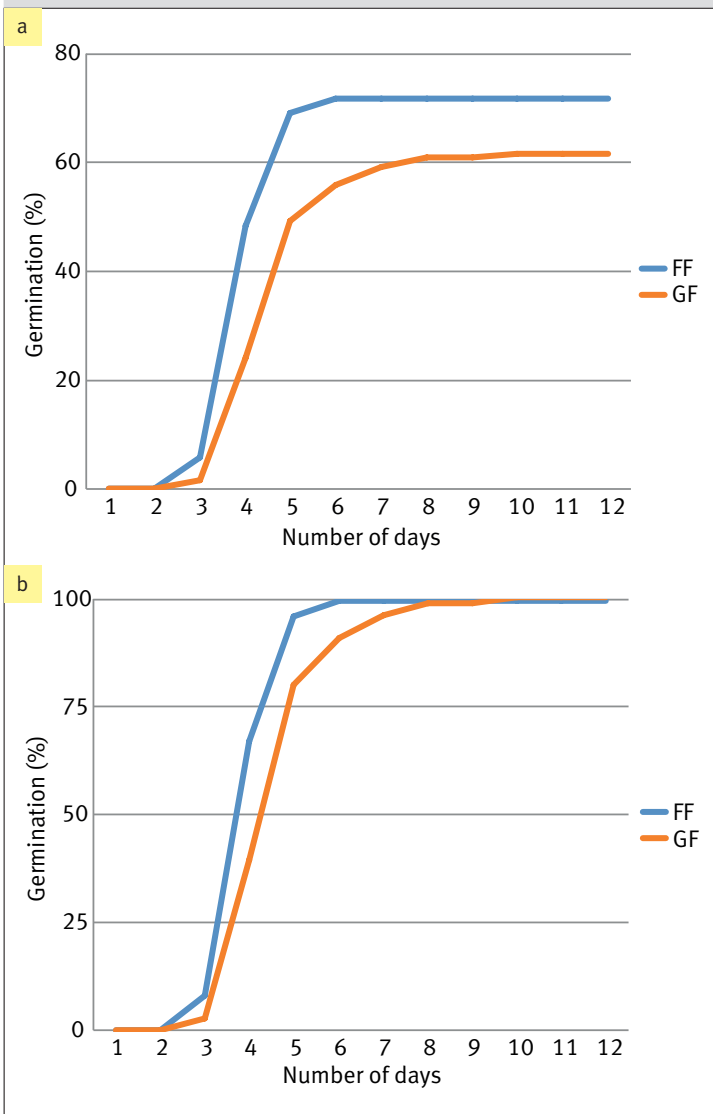


Figure 2.
Germination power of *A. madagascariensis* seeds from floating fruits (FF) and ground fruits (GF): (a) cumulative germination rate relative to number of seeds sown; (b) germination dynamic: cumulative germination rate relative to number of seeds germinated at end of experiment.

The average number of apparently intact seeds in the FF was far less than in the GF: 32 ± 13 at Anjiabe, compared to 102 ± 17 at Anjamangirana. More than 40% of the seeds from the GF collected at Ambatonjanahary were infected with weevils, whereas none of the apparently intact seeds from FF showed any signs of infection by predators.

Germination capacity of seeds

Germination capacity of the FF seeds was not significantly different from that of the GF seeds, 72% to 62% ($t=1,424 < t_{0.975}=2,776$) (figure 2a) (photo 6). Figure 2b shows that the germination rate of seeds from FF was greater than that of the GF seeds: on the fourth day the percentage of germinated seeds (relative to the total number of seeds germinated at the end of the experiment) was 67% for the FF and only 39% for the GF (significant difference: $t=3,180 > t_{0.975}=2,776$). This would indicate that contact with sea water enables more rapid germination of seeds of *A. madagascariensis*. This observation reflects the results of various authors who have shown that subjecting seeds to osmotic treatment, known as priming, can encourage and ultimately accelerate their germination (HEYDECKER *et al.*, 1973; HEYDECKER & GIBBINS, 1978). In experimental conditions, priming can be obtained by soaking seeds in solutions of polyethylene glycol or saline solutions (AFZALL *et al.*, 2008), in limited concentrations, for example, 100mM for *Prosopis juliflora* (NASR *et al.*, 2012). In the floating fruits, this increase in osmotic pressure could have two origins: solubilisation of the sugar rich pulp (OSMAN, 2004) or penetration of sea water into the fruits. However, it is not possible from the results of this study to make such hypotheses.

Effect on germination of the site where fruits wash up

The germination substrate has a strong influence on the germination capacity of seeds. Figure 3 shows that very salty substrates (beach sand and tidal zone limit) are unfavourable to the survival of seeds of *A. madagascariensis*, whether FF or GF: 12 days after sowing no germination had been recorded and a large proportion of seeds were necrosed, significantly more for seeds of FF than GF ($\chi^2_{obs} = 9.77 \geq \chi^2_{0.95} = 3.84$).

The only germinations recorded were from sowings made in soil collected 25m beyond the tidal zone limit and the control substrate, with two observations:

- seeds from FF germinated significantly better than those from GF seeds ($\chi^2_{obs} = 18.24 \geq \chi^2_{0.95} = 3.84$).
- seeds from FF germinated significantly better in the soil collected 25m beyond the tidal zone limit with a light salt content (0,63g/kg equivalent NaCl) than in that of the control substrate ($\chi^2_{obs} = 11.32 \geq \chi^2_{0.95} = 3.84$).

It would appear that seeds from FF germinate better than seeds of GF. These observations support the hypothesis that a priming effect which encourages germination of seeds develops during the period of time the pods spend drifting at sea. It would also seem that a slightly saline substrate is favourable to the germination of *A. madagascariensis*. These conditions seem to come together at the strandline, just above the high tide zone, yet are subject to marine influences.

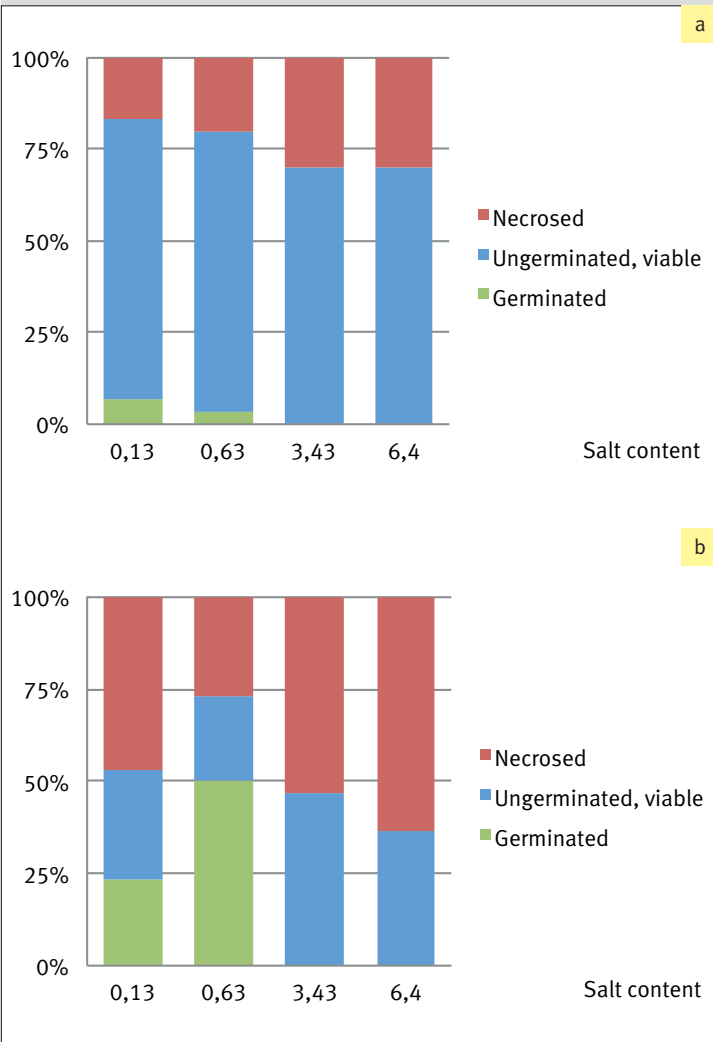


Figure 3. Influence of substrate salinity on the germination capacity of seeds from *A. madagascariensis*. Condition of seeds 12 days after sowing on different substrates of varying salt contents, sampled from river (control), 25 metres from the tidal zone, at the tidal zone limit and on the beach: (a) ground fruits; (b) floating fruits.



Photo 7
Adansonia madagascariensis on the shoreline at Ankify.
Photo C. Cornu.

Discussion

Hydrochory has been studied in tropical forest species but in general only taking into consideration the floatability of seeds and their subsequent germination (LOPEZ, 2001), whereas the present analysis concerning *Adansonia madagascariensis* relates to the dispersal of the fruits. The present observations *in situ* can nonetheless not exclude that the seeds, whose floatability has been verified, might be diaspores.

The results of the present experiments show that marine dispersal is possible for *A. madagascariensis*. The geographic coastal distribution of the species (photo 7, figure 1), its presence along water courses indicates, at least partially, that it is dependant on water. The floatability potential of its fruits associated with a low volume, its shape adapted for barochory² and hydrochory, the salt-resistance of its seed coat associated with the aptitude of its seeds to germinate in a slightly saline soil are all strong indicators that the fruits and seeds of *A. madagascariensis* are adapted to marine hydrochory. The results obtained in this study limit this hypothesis. They show that the fruits of *A. madagascariensis* are apt at floating and therefore capable of ensuring the transport of seeds over long distances. During this drifting phase, the environment of the seeds within the fruits evolves: entry of sea water, solubilisation of pulp. These changes can have positive effects on the viability of the seeds: elimination of parasites and predators like weevils, elimination of parasite-infected seeds, improvement of germination by priming effect due to the increase in osmotic pressure within the pod. However, and as pointed out by SCARANO *et al.* (2003) with *Carapa guianensis*, it is very likely that an extended period of time immersed in sea water might prove harmful to seeds, as prolonged contact with salt could become toxic.

Nonetheless, the presence of a few species *A. madagascariensis* on the beaches of Mayotte at Dapani and Mliha (CHARPENTIER, 2006) would indicate that the seeds may be able to survive long enough for the dominant currents in the north part of the Mozambique Channel (figure 1) (DONGUY & PITON, 1991; SÆTRE & DA SILVA, 1984) to ensure the transport of the fruits and viable seeds to the shores of the Comoro Islands. This observation supports the conclusions of PASCAL *et al.* (2001) who showed that the flora of Mayotte most likely resulted from several successive waves of migration either from Africa, or from Madagascar, and that various introductions are recent, particularly those coming from Africa. From the results of the present study, it is possible to supplement the list of recently introduced species to Mayotte established by PASCAL *et al.* (2001), with the addition of *A. madagascariensis*.

Whilst current estimates of the phylogeny of *Adansonia* by BAUM (2003), based on DNA sequence data and morphology, indicate that African, Australian and Malagasy baobab groups have derived from a common ancestor, the dates are nonetheless approximative. This evolution occurred between 9.4 and 10.5 million years ago, thus eliminating the hypothesis of a Gondwanian origin of baobabs, whose recent emergence occurred 58 million years ago (BAUM, 2003). This recent evolution militates for a marine hydrochory.

² The dispersal of seeds, spores, or fruits by gravity.

Conclusion

This study shows that time spent at sea by fruits of *A. madagascariensis* does not affect the germination potential of their seeds and that germination is possible, and even enhanced, in tidal zones. These results confirm the hypothesis of a marine hydrochory for this species. They show that baobab fruits can remain in the sea whilst maintaining viable seeds capable of colonizing new areas. Thus explaining the frequent occurrence of this species along the coast of Madagascar and, less frequently, on the Mayotte coast. It would be interesting to study the marine hydrochory potential of other species of genus *Adansonia*, attempting to provide some understanding of the very specific current geography of this genus across the world. The presence of a native species in Australia, *A. gregorii*, far from the eight other species may also be explained by an ancient marine hydrochory.

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