

# Removal and predation of aril-covered seeds: the case of *Afzelia bipindensis* (Fabaceae – Detarioideae)

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**Background and aims** – Most tree species with aril-covered seeds are assumed to be dispersed by frugivores. However, the number of studied African rainforest plant species remains low. This study focused on *Afzelia bipindensis*, an important timber species, which produces seeds partly covered by an aril. Specifically, this study aimed to: (1) identify the dispersers and the predators of *A. bipindensis* seeds, (2) characterize the role of those dispersers and predators in the regeneration process, and (3) understand the role of the aril in seed germination in relation to the feeding behaviour of the identified dispersers.

**Methods** – The study took place in a Gabonese evergreen rainforest in 2015 and in a Cameroonian semi-deciduous rainforest in 2016 and 2017. We conducted more than 100 hours of direct observations, and used camera traps to monitor animal activities for 3000 hours within the canopy and 10 000 hours on the ground under fruiting trees.

**Key results** – Three rodent taxa (*Cricetomys emini*, *Funisciurus isabella* and an undetermined species of Muridae) were mainly observed interacting with the seeds but neither birds nor monkeys were observed. Rodents removed more than 90% of the seeds, after detaching the aril, to probably cache them in burrows or superficial caches. Seeds from which we manually removed the aril (mimicking rodent behaviour) had a higher germination rate.

**Conclusions** – Rodents may play a more important role than expected in the dynamics of tree species producing aril-covered seeds.

**Keywords** – Seed dispersal; seed predation; Cameroon; Gabon; *Cricetomys emini*; rodent.

## INTRODUCTION

Plant dispersal patterns are highly influenced by the identity of its vectors. Between 70 and 90% of forest tree species in the tropics are predominantly dispersed by animals (zoochory: Poulsen et al. 2002; Chapman et al. 2010; Markl et al. 2012; Beaune et al. 2013a, 2013b; Beckman & Rogers 2013). Although the role of large mammals and birds in seed

dispersal is widely recognized, the role of rodents is much less studied (Jansen et al. 2002; Steele et al. 2011; Hirsch et al. 2012; Evrard et al. 2017): they are often considered as predators though they may contribute to secondary seed dispersal (Forget & Milleron 1991; Steele et al. 2011). Rodents collect seeds and cache them by larder hoarding, when the animal stores its food in one large cache, or by scatter hoarding, whereby the food is divided into multiple small caches

below the ground surface. Although most seeds hidden by rodents are eaten in the coming weeks or months, some can be forgotten and may germinate under favorable conditions (Evrard et al. 2017). Specifically, seedling establishment depends on the actions of the rodent: what is eaten, what is cached, where and for how long (Feer & Forget 2002; Steele et al. 2011).

Post-dispersal predation affects the recruitment dynamics of seedlings (De Steven & Putz 1984; Sork 1987; Feer & Forget 2002), and therefore plant community dynamics (Moupela et al. 2013). Predators can be specialized to predate only one species (Liu et al. 2012) or phylogenetically related species (Novotny et al. 2002; Agrawal & Fishbein 2006; Gilbert & Webb 2007). Furthermore, they are generally found in areas of high seed or seedling density, often next to the mother tree (Janzen 1971). Therefore, survival chances are generally considered optimum at a certain distance from a parent tree, where seed or seedling density is lower and predators less abundant (Schupp & Jordano 2011).

In the case of some aril-covered seed species, it has been shown that canopy-dwelling primates and birds can play a major role in primary dispersal (Gathua 2000; Russo 2003; Boissier et al. 2014; Trolliet et al. 2017). Indeed, primates consume the aril and spit out the seed, whereas birds (hornbills in particular in Central Africa) generally swallow the entire seed and deposit it intact under their nesting or resting spot (Kitamura 2011). Generally, aril-covered seed species are typical of the bird-monkey dispersal syndrome (Gauthier-Hion et al. 1985). However, once the seed reaches the ground, with or without its aril, rodents, such as *Cricetomys emini* (the Emin's pouched rat), may remove it (Beaune et al. 2012). This implies that the role of rodents in the dispersal of aril-covered seeds might be more important than previously considered (Evrard et al. 2017). In other cases, it has been shown that there can be differences between the dispersal syndromes of similar aril-covered seeds. For example, the Asian species of the genus *Azelia* Sm. are mostly dispersed by water (hydrochory) whereas in Africa, zoochory seems to be the major dispersal mode of this genus (Snow 1981).

This study aims to improve knowledge of aril-covered seed dispersal in Central Africa, using *Azelia bipindensis* Harms as a study case. Our specific objectives were to: (i) identify dispersers/predators of *A. bipindensis* with direct and indirect observations on the ground and in the canopy, and (ii) describe the impact of aril removal on germination success.

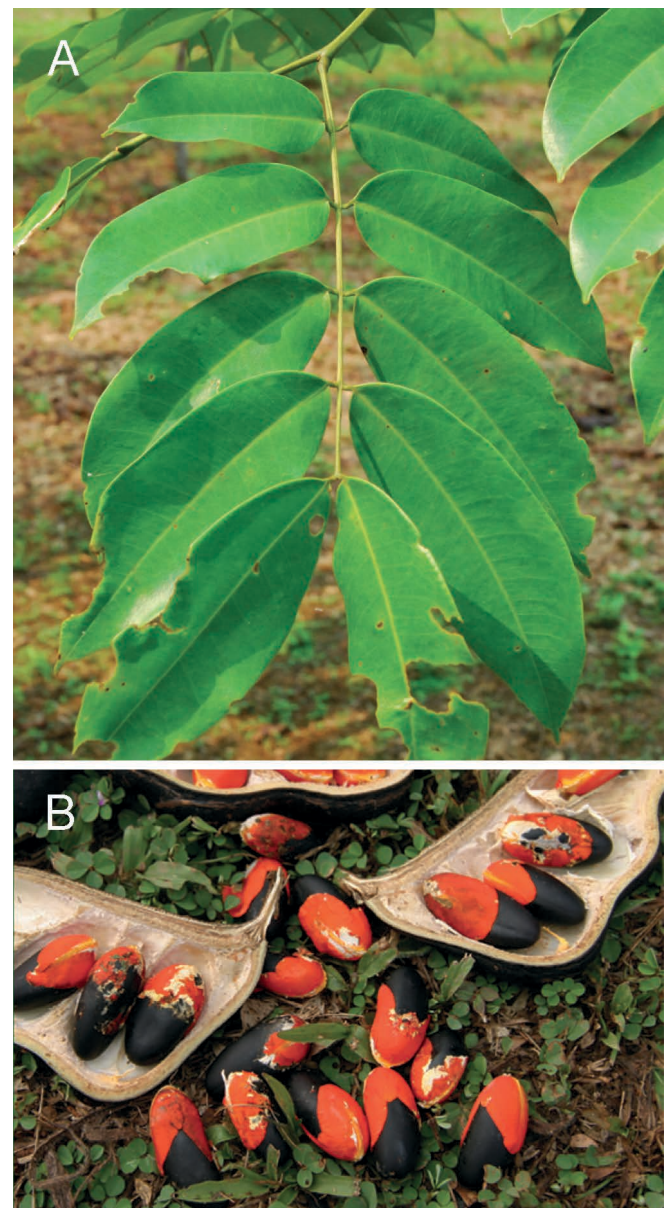
## MATERIAL AND METHODS

### Study species

*Azelia bipindensis* Harms (Fabaceae – Detarioideae) is an African endemic species found in tropical rainforests from the Guineo-Congolian region with a disjunct distribution between adjacent subregions (Doucet 2003; Donkpegean et al. 2014). It ranges from Ivory Coast to Democratic Republic of Congo (Gérard & Louppe 2011). *Azelia bipindensis* can grow to more than 150 cm dbh (diameter at breast height) (Chudnoff 1980) with a total tree height reaching between 40 and 50 m (Donkpegean et al. 2014).

*Azelia bipindensis* is a non-pioneer light-demanding species with a slow growth rate. It is a hermaphrodite species with fertile flowers appearing when dbh  $\geq 20$  cm. The flowers are characterized by a unique white petal ( $3\text{--}4.5 \times 2\text{--}2.5$  cm) glabrous on the external side. The petal colour changes to purple once the flower has been fertilized. The fruits are large, ovoidal, woody pods ( $11\text{--}19.5 \times 5.5\text{--}8$  cm) containing 3 to 4 black seeds ( $2.5\text{--}4.5$  cm in length) encased in a red aril forming two unequal lobes (CTFT 1980; Donkpegean et al. 2014; fig. 1).

*Azelia bipindensis* is a highly disseminated species (fewer than two trees per hectare for a dbh  $\geq 20$  cm) and is considered vulnerable on the IUCN Red List (Donkpegean et al. 2014). The species has a high commercial value due to the



**Figure 1** – Leaves (A) and seeds (B) of *Azelia bipindensis* (from Meunier et al. 2015, distributed under the terms of the Creative Commons attribution license, CC BY 4.0).

quality of its wood, which is marketed as doussié or afzelia (Donkpegan et al. 2014).

### Study sites

This study was conducted over three years (2015–2017), in two FSC (Forest Stewardship Council) certified forest concessions: one in Gabon for the first study year and the other in Cameroon for the latter two study years. Observations were conducted during the fruiting period of *A. bipindensis* in 2015 (February–March) in Gabon, and in 2016 and 2017 (July–August) in Cameroon. The differences in phenology between the study sites are due to the difference of latitude.

The Gabon concession is managed by Precious Woods Gabon – Compagnie Equatoriale des Bois (PWG – CEB) and is situated at Bambidie, close to Lastoursville (between 0°30'–1°00'S and 12°30'–14°00'E). The forest is evergreen and the climate is characterized as equatorial with annual precipitations of around 1700 mm (TeREA 2007; Moupela et al. 2013). The landscape comprises large plateau and hill assemblages marked by many rivers at an average elevation of 700 m with some considerable slopes (TeREA 2007). The soils are characterized as typical ferrallitic (Mapangou 2004).

The Cameroon forest concession is managed by Pallisco and is situated at Mindourou, around 60 km from Abong-Mbang (between 3°01'–3°25'N and 14°05'–14°31'E) in the southeast of Cameroon. The forest is semi-deciduous. The

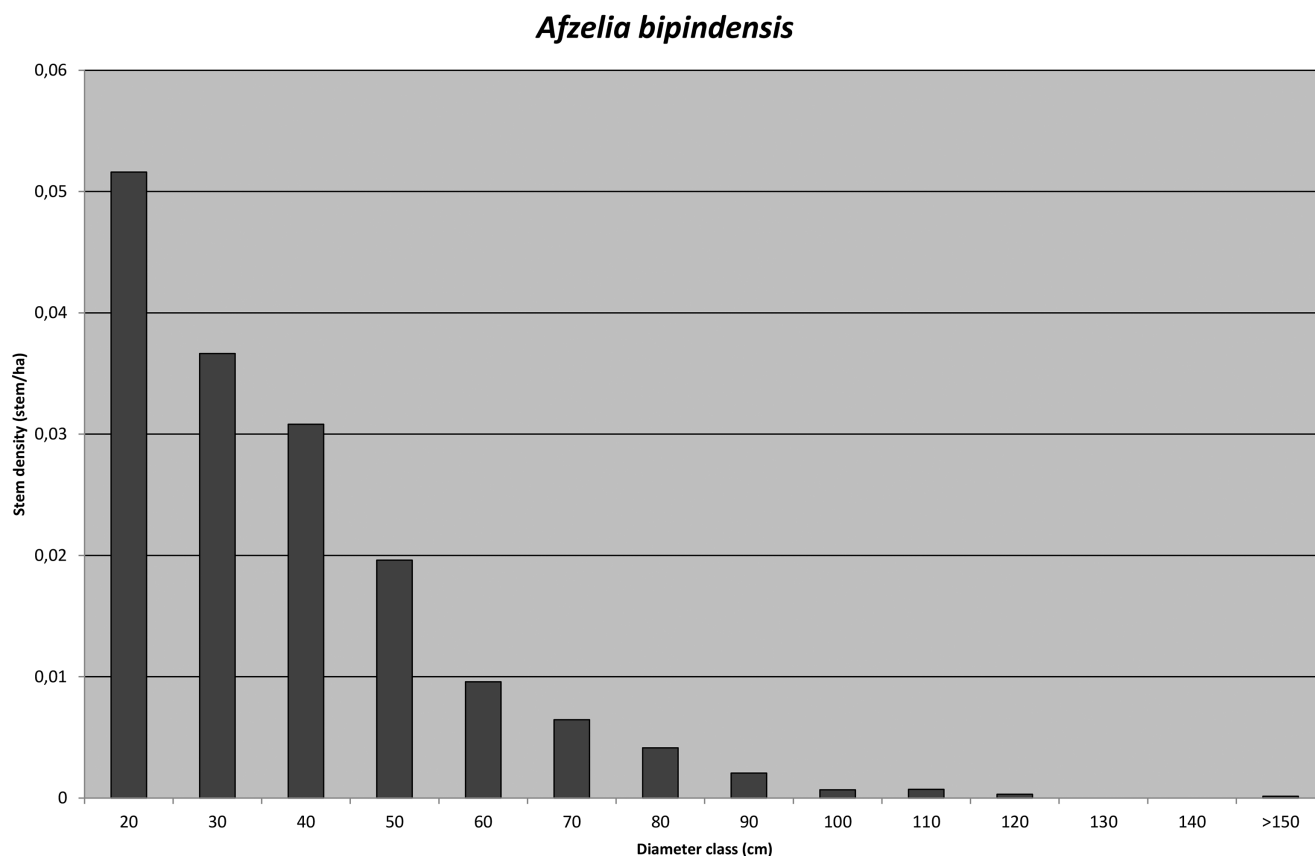
annual rainfall is 1626 mm, the seasons are inversed compared to Gabon (Bourland et al. 2012; Vleminckx et al. 2014). The soils are characterized as ferrallitic red or typical yellow (Kouadio & Doucet 2009). Subsequently, the two sites will be called Bambidie and Mindourou, respectively.

As an overview of the species population dynamics, stem diameter distributions of *A. bipindensis* at both sites were obtained from inventories performed by the logging companies. The curves are similar and the abundance of small diameter stems indicates a good regeneration (fig. 2) no matter the identity of the potential dispersers.

Animal communities seemed mostly undisturbed by logging activities at Bambidie. The densities of mammals were similar to the ones found in an adjacent protected area (Haurez et al. 2013). At Mindourou, due to higher human densities close to the logging concessions, some poaching activities occurred in the past. The densities of large mammals are lower at Mindourou than at Bambidie, but small primates and large birds that might play a key role in the dispersal of *A. bipindensis* seeds given their physical traits (Gartlan & Struhsaker 1972; Bationo et al. 2000), are still abundant (Fonteyn 2017).

### Dispersal and predation of *A. bipindensis* seeds

Direct and indirect (camera traps: Bushnell TC Aggressor HD) observations were made on the ground and in the canopy (approx. 40 m above the ground level) of a total of 14



**Figure 2** – Combined stem diameter distribution of *Afzelia bipindensis* in Precious Woods Gabon – Compagnie Equatoriale des Bois (PWG – CEB) and Pallisco forests according to their inventory (data from Demarquez & Jeanmart 2004 and Nature+ & Pallisco 2012).



**Table 1 – Number of trees observed, hours of observation and camera-days per site and year.**

		Bambidie	Mindourou	
		2015	2016	2017
<b>Number of trees observed</b>		6	5	4
<b>Ground</b>	<b>Direct</b>	/	/	/
	<b>Indirect (camera traps)</b>	262 camera-days at 3 trees	76 camera-days at 5 trees	105 camera-days at 4 trees
<b>Canopy</b>	<b>Direct</b>	101 hours at 3 trees	/	/
	<b>Indirect (camera traps)</b>	/	/	126 camera-days at 4 trees

different focal trees (6 in Gabon, 8 in Cameroon, one being observed 2 years in a row) to identify the animals involved in seed dispersal and predation, and to characterize their behaviour. Table 1 summarizes the observation methods and the number of trees observed per site and year. All trees were selected on the basis of the logging company inventories and the trees' fructification status. Moreover, observations were made on trees that were at least 1.5 km apart to ensure independent observations. This approach allows an estimation of the attendance rate of trees (Rovero et al. 2010; Mugerwa et al. 2012; Jansen et al. 2014). Camera traps can be set to take photographs or videos of animals using an infrared movement sensor (Mohd Azlan & Lading 2006), which also enables the capture of nocturnal dispersers and/or predators (Moupela et al. 2013; Jansen et al. 2014; Meek et al. 2014). For the current study, camera traps were set to take a photograph of the detected animal at the beginning of each observation period, and were subsequently changed to 30-sec video mode in the last week of each observation period, to enable characterization of animal feeding behaviour. The camera traps were programmed to take three photographs when movement was detected.

At Bambidie, direct observations of the fruits in the canopy took place at three trees using binoculars, totaling 101 hours, to determine the animals visiting and the number of seeds removed. Furthermore, two camera traps were directed towards three other focal fruiting trees where a sample of 20 bait seeds was placed on the ground for a total of 262 camera-days (table 1). At Mindourou, in 2016, 10 camera traps were placed under five fruiting trees for 27 days following the same methodology as at Bambidie. The following year, camera traps were placed under and in the crown of four fruiting trees, at a mean height of 43 m and were left in place for a total of 126 camera days.

Each animal detected by camera traps was classified as a primary disperser, secondary disperser or predator on the basis of their behaviour observed in camera trap videos from the last week of observation. Primary dispersers were determined as those observed to swallow or store the entire fruit and seed in their pouches, picking it directly from the branches of the tree. Secondary dispersers were observed to transport seeds intact after a first dispersal event (seeds on the ground). Predators directly consume seeds in front of the camera, thus eliminating any chance of germination.

### Feeding behaviour of rodents and impacts on the germination of *A. bipindensis* seeds

To understand the impact of aril removal by rodents, an experiment was carried out in 2015 in Gabon using a sample of 336 seeds divided into two treatments: seeds intact with aril (control seed) and seeds without aril (removed manually). Seeds were sowed immediately after collection in a nursery installed in the base camp of the forest company on a homogenous substrate. To avoid any bias linked to light exposure, seed positions were randomized at the beginning of the experiment. The same homogenous substrate (top soil of the forest) was used. Seed germination was monitored every day during 6 weeks after sowing.

### Data analysis

Data collected by camera traps were encoded to record the GPS coordinates of the trap, date and time of detection, observed animal species and behaviour (consumption of bait, removal of baits or no action concerning the bait). To ensure independence of observations, presence events were defined as detections of a species occurring at least 30 minutes apart (Cadman & González-Talaván 2014). If the same species passed in front of the camera several times in less than 30 minutes, a mean observation time was calculated using circular statistics.

Circular statistics were also used to identify the mean duration of activity of the most represented animals, using the "CircStats" package of R 3.0.2® software. The exact times of each animal observation were converted to angles between 0 and  $2\pi$ . Firstly, data points (between 0.00 and 23.98, respectively, corresponding to the times 0:00 and 23:59) were assigned to each observation time. Secondly, this  $[0; 24[$  interval was transformed into a  $[0; 360[$  interval with a simple multiplication of the values by 15. These values were transformed to radians and the mean angle corresponding to the direction of a vector inside a circle was calculated. The resulting angle was then transformed back into numerical time to obtain the mean preferred activity hour of the observed animal. The length of the vector (between 0 and 1) corresponded to the aggregation rate of the animal activity around the mean angle (= the mean activity hour). In other words, the closer the value was to 1, the more the data were aggregated around the value of the determined mean time. A

**Table 2 – Observed animal species next to the seeds of *Afzelia bipindensis* at Bambidie (2015) and Mindourou (2016 and 2017) by ground-level camera trapping.**

In the “seed manipulation” column, “0” means no manipulation, and “1” means that the seed was taken away. We determined the p-value with a Rayleigh test to characterize the significance of the animal activity. R is the aggregation rate of the animal activity; the closer the value is to 1, the more the data were aggregated around the value of the determined mean time. The p-value represents the aggregation rate is very highly significant (\*\*\*), highly significant (\*\*), significant (\*), or not significant (NA). The percentage on the “species” column represents the proportion of the animal detection among all of the detections for both study sites.

Groups	Events of animal presence				Animal activity			Seed manipulation
	Species	2015	2016	2017	Mean time of activity (hours:min)	R value	p-value	
Rodents	<i>Atherurus africanus</i> (0.88%)	2	1	6	00:25	0.9852	***	1
	<i>Cricetomys emini</i> (41.31%)	150	44	89	22:37	0.9879	***	1
	<i>Funisciurus isabella</i> (7.88%)	18	15	21	10:52	0.998	***	1
	<i>Protoxerus stangeri</i> (2.04%)	7	3	4	10:49	0.9984	***	1
	Undetermined Muridae (39.85%)	219	34	20	00:13	0.9878	***	1
Ungulates	<i>Cephalophus dorsalis</i> (0.58%)	3	1	0	23:37	0.9845	*	0
	<i>Cephalophus</i> sp. (0.44%)	0	0	3	00:27	0.9905	*	0
	<i>Philatomba congica</i> (2.19%)	0	0	15	11:46	0.9964	***	0
Birds	<i>Alethe diademata</i> (0.58%)	4	0	0	09:27	0.9993	**	0
	<i>Francolinus</i> sp. (1.75%)	10	2	0	14:24	0.9962	***	0
	<i>Tropicranus albocristatus</i> (0.15%)	1	0	0	NA	1	NA	0
Pholidota	<i>Uromanis tetradactyla</i> (0.58%)	1	3	0	21:10	0.9998	*	0
Carnivores	<i>Genetta</i> sp. (0.88%)	3	1	2	20:13	0.9941	*	0
Total		418	106	161				

Rayleigh test was performed to verify that the animal activity was significant (Davies & Ashton 1999).

The results of the germination experiments were analysed using the software R 3.0.1© after verifying the application conditions, to describe the feeding behaviour of rodents and the impact on germination of *A. bipindensis* seeds.

## RESULTS

### Predators and dispersers of *A. bipindensis* seeds

Although more than 10 000 photographs were taken by the camera traps positioned in the canopy at Mindourou, no animal activity was observed. Instead, all photographs were a result of camera traps being triggered by branches moving in the wind. This is confirmed by the direct observations conducted at Bambidie where no animal was directly observed consuming *A. bipindensis* seeds in the canopy during the study period. In contrast, ground-level camera traps detected a total of 685 events of animal presence, involving 14 animal species, nine of which were observed in both sites (table 2).

The predominant taxa of animals observed were rodents. The most common species was the pouched rat (*Cricetomys emini* (Wroughton, 1910) (fig. 3A)), found to be mostly active at night with a mean time of activity around 23:00. Other

rodents of the Muridae family (fig. 3B), unidentified to species level, were also nocturnal. The squirrel *Funisciurus isabella* (Gray, 1862) (fig. 3C) consumed seeds of *A. bipindensis* around 11:00. When extracting data from videos, it was observed that some rodents (unidentified Muridae) discarded the aril of seeds without consuming it, and then took the seed away, while *C. emini* was always observed to remove the seed complete with its aril. Other species that handled the remaining 10% of the seeds on the ground either consumed it directly (*Atherurus africanus* Gray) or transported the seeds away from the tree (*Protoxerus stangeri* Waterhouse). Duikers (*Cephalophus* spp. Smith) and monkeys (*Cercocebus agilis* Milne-Edwards) paid no attention to the seeds.

In the experiment, the presence of the aril significantly lowered the germination rate. The germination rate increased from 41.7% to 55.4% when the aril was removed and the difference between treatments was significant (Fisher's F-test = 6.116, p-value = 0.014).

## DISCUSSION

Rodents accounted for more than 90% of camera trap observations. This suggests that rodent species play a key role in the fate of *A. bipindensis* seeds. The most frequently ob-

served species was *Cricetomys emini*. The feeding behaviour of this nocturnal species is still to be defined and can either be larder or scatter-hoarding (Nyiramana, 2012; Aliyu et al. 2014; Rosin & Poulsen 2017). Nocturnal Muridae were also observed. Unlike *C. emini*, they sometimes removed the seed arils before moving them. This may improve and accelerate germination as observed in our experiment. Because of the small amount of seeds that they can carry, Muridae are characterized by a scatter-hoarding feeding behaviour (Soné & Kohno 1999; Soné 2004; Zhang et al. 2008). This behaviour implies careful selection of cache placement to avoid any cache pilferage. Rodents exhibiting this behaviour usually select less frequented zones, with low densities of conspecifics

(Swartz et al. 2010; Muñoz & Bonal 2011; Hirsch et al. 2012; Steele et al. 2014). Two species of squirrels, *Funisciurus isabella* and *Protoxerus stangeri* (Waterhouse, 1842), moved seeds without first removing the aril. *Funisciurus isabella* is considered as a predator and an occasional disperser thanks to its scatter-hoarding behaviour (Beaune et al. 2013b; Haurez et al. 2015; Tosso et al. 2017). *Protoxerus stangeri*, a big squirrel, is supposedly a larder-hoarder, storing all the collected seeds in one big cache that is vigorously defended (Luo et al. 2014). However, both squirrel species have also been observed (Kankam & Oduro 2009) consuming directly the fruit pulp of *Antiaris toxicaria* Lesch. (Moraceae) and dropping the seed under the parent tree in the Bia Biosphere Reserve (Ghana).

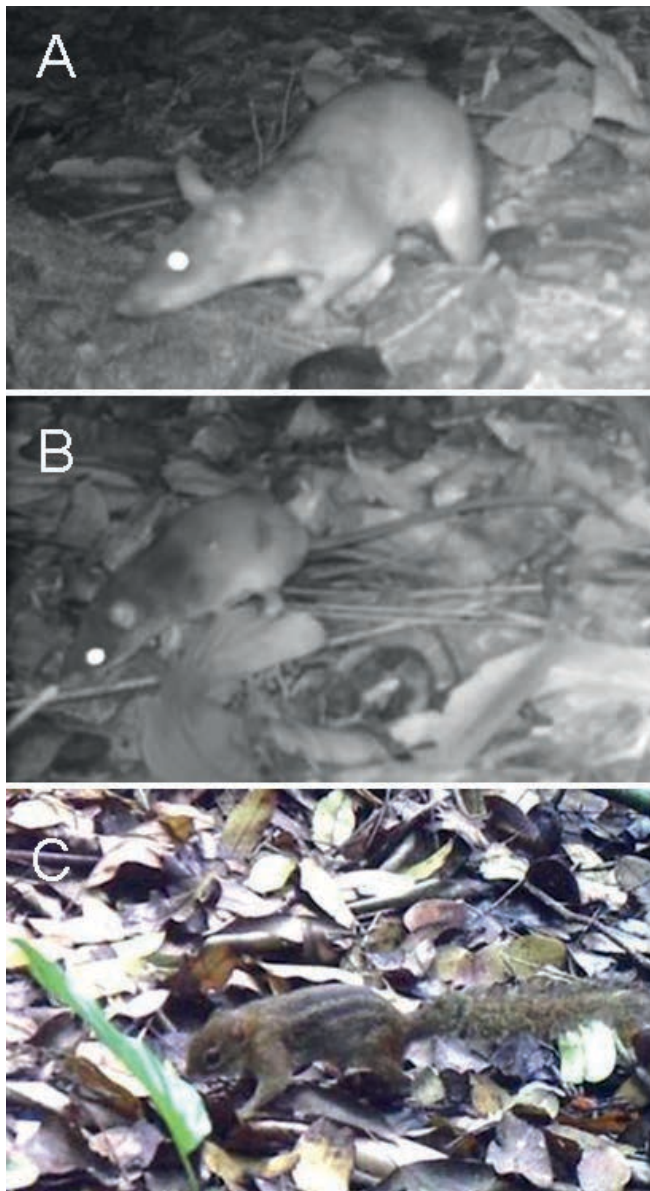
Bationo et al. (2000) also suggested that rodents can play an important role in the fate of *Azafia* seeds. They showed that more than 90% of the seeds of *A. africana* Sm., found in Sudanian woodlands, disappeared once the ground was fully cleared by natural fires. They suggested rodents to be the main actors and to exert high predation levels.

The ecological role played by rodents is linked to the temporal and spatial variability of the availability of food resource (Jansen et al. 2004; Moore et al. 2007; Gálvez et al. 2009). This affects direct consumption, seasonal caching rates and the spacing of caches (Gálvez et al. 2009; Haugaasen et al. 2010).

Hirsch et al. (2012) demonstrated that some rodent species can transport seeds to locations with low densities of plant conspecifics, to avoid cache pilfering by other rodents. They disperse seeds up to a distance of 100 m and thus prevent a clumped distribution of trees (Jansen et al. 2012). This can lead to regeneration of the species and can account for the random distribution of species with a low density of adult trees. Indeed, seeds dispersed by rodents and buried in the ground could germinate, but it depends upon the depth at which they are buried (Rosin & Poulsen 2017).

No animal was observed interacting with *A. bipindensis* seeds in the canopy, either in Gabon or Cameroon. This suggests that the bird and primate species observed in the canopy of other *Azafia* species (Gathua 2000) probably play only a marginal role in the dispersal of *A. bipindensis* seeds. Gathua (2000) studied the animals interacting with the seeds of *A. quanzensis* Welw., a species of Zambesian woodlands whose seeds are morphologically similar, but with a thicker aril than in *A. bipindensis*. He observed three animal taxa (recorded as “baboons”, “monkeys” and “squirrels”) interacting with the fruits in the canopy. Primates interacted with 73.3% of the seeds produced by all focal trees.

The absence of primate observations in the present study could be surprising. Monkeys have been observed to consume the arils of *A. quanzensis* and *A. africana* and to spit out the seed at a certain distance from the fruiting tree (Schupp 1993; Harrison 1983; Gathua 1992, 2000; Bationo et al. 2000; Goodwin 2007). In both sites, some primate species were present at relatively high densities (Muchaal & Ngandjui 1999; Poulsen et al. 2001; Haurez et al. 2013; Koerner et al. 2016). Although it has been demonstrated that large primates can ingest aril-covered seeds from Myristicaceae or Fabaceae (Rogers et al. 1990; Tutin & Fernandez



**Figure 3** – The main consumers of *Azafia bipindensis* seeds with (A) the pouched rat (*Cricetomys emini*), (B) unidentified Muridae, and (C) Lady Burton's Rope Squirrel (*Funisciurus isabella*) (© Quentin Evrard, distributed under the terms of the Creative Commons attribution license, CC BY 4.0).



1993; Nishihara 1995; Watts et al. 2012; Beaune et al. 2013a; Serckx et al. 2015), the seeds of *A. bipindensis* were never observed in gorilla dung (Hauzeur et al. 2017). However, occasional consumption cannot be excluded since primate species may only forage for these arils when more energetic food resources are scarce, as observed for another Fabaceae species (Dohu et al. 2018).

The terrestrial hornbill (*Tockus* spp.) was suggested to act as the main disperser of *A. africana* (Bationo et al. 2000). In this study, no consumption by hornbills was observed despite their presence around the focal trees. Poulsen et al. (2002) studied the diet of hornbills in Central African rainforests where *Afzelia bipindensis* has been inventoried (Sonké 1998). They did not record any consumption of *Afzelia* seeds. Moreover, although Gathua (1992) suggested that hornbills may play a role in the dispersal of *A. quanzensis* seeds, and the same was suspected by Snow (1981), no such interaction was observed.

Finally, it is necessary to consider the possibility of dispersal modes other than zoochory. It is possible that seeds left intact under the mother tree germinate and produce viable juveniles since they can survive in moderate shade (Donkpegan 2017). However, the spatial distribution of this species within the study sites does not support this hypothesis (Donkpegan et al. 2014). Hydrochory might account for some seed dispersal, as it is known to occur in most Asian *Afzelia* species (Ridley 1930). The preference of *A. bipindensis* for river banks has been observed by Allaer (2017) in Cameroon, although the species also occurs at other locations.

## CONCLUSION AND PERSPECTIVES

The stem diameter distribution of *A. bipindensis*, its non-clumped distribution and the abundance of saplings suggest an effective contribution of agents involved in the regeneration of the species.

While aril-covered species are typical of the bird-monkey dispersal syndrome (Gauthier-Hion et al. 1985), this study demonstrates that, in the case of *A. bipindensis*, neither birds nor monkeys seem to play an important role in its dynamics. In fact, only rodents were observed interacting with the seeds, and although they are often considered predators, they might also disperse seeds by larder or scatter hoarding (Janzen et al. 2012; Evrard et al. 2017).

The aril characteristics probably play a crucial role in plant-animal interactions. The aril of *A. bipindensis* is very thin and may be low in nutrient content. Furthermore, it may contain toxic compounds such as alkaloids, non-protein amino acids or flavonoids (Janzen et al. 1990). In support of this, some rodent species were observed in the present study discarding the aril from the seed. Complementary studies are thus required to further investigate this subject.

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