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ORIGINAL ARTICLE

Do flying foxes limit flower abortion in African baobab (*Adansonia digitata*)? Case study in Benin, West Africa

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Abstract – Introduction. The plant baobab (*Adansonia digitata* L.) is a multipurpose tree in Sub-Saharan Africa. This study investigates the role of bat-induced pollination in baobab fruiting. **Materials and methods.** The tree was studied in three different climatic regions in Benin Republic: Matéri, Dassa-Zoume and Come-Houéyogbé, representing the Northern, Central and Southern parts of the country, respectively. Tree size (diameter at breast height, height, crown diameter) and flower size (sepals and petals length and width) were measured from each of the trees in the study areas and flower visitation by bats was monitored. Bats' contribution to pollination success was also evaluated by monitoring caged and free flowers. **Results and discussion.** There were significant differences in tree and flower sizes among the three regions. Significant differences were also observed in the mean number of bat visits per tree and pollination success among tree populations, but, fruit set per tree was not significantly different among baobab populations, at least in the first 8 weeks. In all populations, flower abortion was significantly elevated in caged flowers. **Conclusion.** Based on findings of this study, it can be concluded that bat-pollination increases the fruit set rate, making it an important factor for *in situ* regeneration of baobab trees in the country.

Keywords: Benin / baobab / *Adansonia digitata* / flying fox / bat pollination / fruiting

Résumé – Les chauves-souris contribuent-elles à limiter l'avortement des fleurs chez le baobab d'Afrique (*Adansonia digitata*) ? Étude de cas au Bénin, en Afrique de l'Ouest. Introduction. Le baobab (*Adansonia digitata* L.) est un arbre à usages multiples en Afrique sub-saharienne. Cet article étudie la pollinisation induite par les chauves-souris sur la fructification du baobab. **Matériel et méthodes.** Les arbres de trois régions climatiques différentes en République du Bénin ont été étudiés : Matéri, Dassa-Zoumè et Come-Houéyogbé, représentant le Nord, la zone centrale et la partie Sud du pays, respectivement. La dimension des arbres (diamètre à hauteur de poitrine, hauteur, diamètre de la couronne) et des fleurs (longueur et largeur des sépales et pétales) a été mesurée à partir de chacun des individus des zones d'étude et la visite des fleurs par les chauves-souris a été surveillée. La contribution des chauves-souris à la réussite de la pollinisation a également été évaluée à partir de fleurs libres ou protégées (en cage). **Résultats et discussion.** Des différences significatives ont été trouvées pour la dimension des arbres et des fleurs entre les trois régions étudiées Des différences significatives ont également été observées pour le nombre moyen de visites de chauves-souris par arbre et pour le succès de la pollinisation entre populations d'arbres. En revanche, la mise à fruit par arbre n'a pas été significativement différente entre les populations de baobab, au moins dans les 8 premières semaines. Dans tous les cas, l'avortement des fleurs a été significativement plus élevé sur fleurs mises en cage. **Conclusion.** D'aprés les résultats de cette étude, on peut conclure que la pollinisation par les chauves-souris augmente le taux de nouaison, ce qui est en fait un facteur important dans la régénération *in situ* des baobabs dans le pays.

Mots clés : Bénin / baobab / *Adansonia digitata* / chauve-souris / pollinisation / fructification

1 Introduction

The African baobab (*Adansonia digitata* L.) is one of the most economically important plant species used in Benin by local communities. Its fruit, leaves and seeds are used for food and other parts of the plant, including bark fibers, are used for medicinal purposes and for a variety of other applications [1–3]. During acute seasonal food supply fluctuations, the leaves and fruit of baobab are of particular importance as

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supplementary food [4]. Additionally, the trade of fruit pulp and kernel of this plant generates substantial income for many local communities.

African baobab trees bear large, white flowers, up to 20 cm in diameter [5], that hang down on long stalks. Flowers open in the late afternoon and they remain open through the night [6]. During this time they receive visits from diverse animals such as ants [7], bush babies [8], bees, flies, butterflies and moths [6,9,10]. However, their primary pollinators are thought to be bats [11–13]. Fruit bats reported as pollinators of African baobab trees are all flying foxes (*e.g.*, *Eidolon helvum*, *Epomorphorus gambiensis Epomophorus wahlbergi Rousettus aegyptiacus*). They are attracted by a strong sour scent emitted by flowers [14]. The pollination of the African baobab occurs over a 16 to 20 h period [15] between dusk and dawn.

Visits by pollinating animals are essential for the majority of angiosperms because they are pollen-limited and rely on animals for sexual reproduction [16, 17]. Apart from the fact that baobab flower morphology is best suited to bat pollination [18], moths and hymenopterous insects also visit baobab flowers [9, 10]. Collectively, these animals help to increase fecundity in baobab as it is presumed that baobabs are self-incompatible [6]. Low fruit-set has been speculated to reflect a form of sexual dimorphism, and the belief in the existence of male and female baobab trees is common throughout Africa [19]. The contribution of flying foxes to effective pollination of African baobab flowers deserves further study given its possible role in limiting the fruit production.

Previous work on the African baobab population's characterization in Benin reported massive flower abortion in the Central region compared with the Southern and Northern regions (Assogbadjo, pers. com.). We thought this could be linked with possible pollination problems in this region. To date, no study has been conducted on the pollination ecology of African baobab in Benin.

The present work aims at assessing the role of pollination services in general, and particularly the role of flying foxes, in increasing fruit production (and reducing fruit abortion) in the targeted baobab populations. We hypothesized that increased bat pollination would be associated with higher fruit production in African baobab in Benin. We compared data collected in different populations to look for correlations between bat pollination and fruiting in this plant.

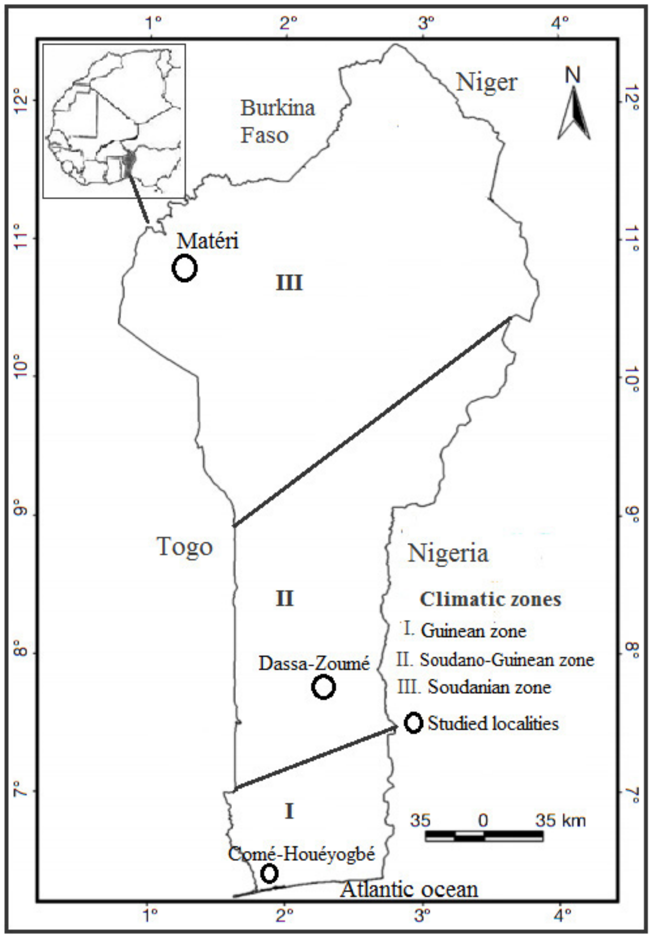

Figure 1. Map of Benin showing the climatic zones and the studied localities.

2 Material and methods

2.1 Study area

The study was carried out in Benin, a western African country located between the latitudes 6°20'N and 12 °30'N and the longitudes 0°45'E and 03°70'E (*figure 1*). Data were collected in the three climatic zones of the country. The Guinean zone (I) is characterized by a bimodal rainfall regime with peaks in April-June and September-November. The mean annual rainfall is 1.200 mm. The temperature ranges from 25 °C to 29 °C and the relative humidity from 69% to 97%. Soils are mainly ferrallitic with hydromorphic soils and vertisols in some localities. The Sudano-Guinean zone (II) or transition zone is characterized by unimodal rainfall, with the annual total varying from 900 mm to 1,110 mm. The rainy season is from May to October. The annual temperature of this zone ranges from 25 °C to 29 °C and the relative humidity from 31% to 98%. Soils are mainly ferruginous. The Sudanian zone (III) has one rainy season ranging from May to October and one dry season from November to April. The temperature varies from 24 °C to 31 °C and the relative humidity from 18% to 99%.

2.2 Data collection

Data collection was conducted from May 2011 to July 2013 covering three different flowering periods in Benin. Baobabs bear flowers mainly just before or at the beginning of the rainy season: March-April-May in the South and May-June-July in the North. In 2011, population-level measurements were made, while the period between the years 2012 and 2013 was used to collect data on flowers, flower visitation, pollination success, and fruit set.

2.2.1 Distribution of baobab trees

Baobab trees are scattered in fallow fields, farmlands and near houses, consistent with the use of their leaves and fruit for food and medicinal use. A number of 658 individuals found in the studied localities that were accessible were systematically measured for their diameter at breast height (DBH), tree height and tree crown diameter.

To measure the DBH of a given baobab tree, a diameter tape (pi-ribbon) was wrapped around the tree, in the plane perpendicular to the axis of the trunk 1.3 m above ground. Tree heights were determined using clinometers. The crown of a tree consists of the mass of foliage and branches growing outward from the trunk of the tree. The average crown spread is the average horizontal width of the crown, taken from one drip line to another as one moves around the crown. When the crown did not fit a circle-like shape, we measured and calculated the mean of the longest and shortest diameter of the tree crown.

2.2.2 Characterization of baobab flower organs

A total of 1,605 flower organs were characterized by measuring the size (length and width) of all 5 (rarely 4) sepals and petals of each selected flower in order to compare the mean values among the studied localities. We focused on these organs because sepals influence nectar production and petals serve as a visual signal and landing space for pollinators. The nectar secretory glands are located on the inner face of sepals at the base of the calyx. Once the sepal or petal is removed, it is opened on a flat surface and measured from one extremity to another on longest (length) and widest (width) axes.

2.2.3 Flower visitation and pollination success

Each evening, freshly opened flowers that were easily observable were located and marked with fluorescent tape. The following morning the same trees were visited to see if the marked flowers had been visited by flying foxes. Proof of visits was revealed by the very visible laceration traces of flying foxes' claws on the white petals. Flying foxes' claws leave many small holes on the petals that become reddish, features easily recognizable in the morning.

Flower wilted by the evening of the day following anthesis. Without successful pollination, the whole peduncle dries out and falls within a few days. When pollination is successful, only the sepals and petals fall, leaving the floral receptacle attached to the peduncle. In such a case, the ovary gradually grows to form a spherical ball that will eventually mature into the fruit. The proportion of open flowers that were visited by bats was recorded daily. The average proportion of visited flowers for a given tree was defined as the visitation rate. After 2 weeks, the proportion of the watched flowers that were still attached and developing as fruit was determined and defined as pollination success.

Figure 2. Freshly opened flower caged with small mesh net to avoid flying foxes contact.

2.2.4 Flying foxes contribution to fruit production in baobab

In order to find out the contribution of flying fox pollination to fruit production, selected visited/lacerated flowers were compared with caged adjacent flowers that opened the same day. *Figure 2* shows the flower caging system that avoided flying fox contact but allowed insects contacts. This monitoring lasted 2–8 weeks. We compared the numbers of maturing fruit on flowers in the two treatments to evaluate the role of flying foxes in fruit set.

2.2.5 Fruit production per locality

About 8 weeks after we started the monitoring of baobab flowers, we counted all maturing fruits remaining on the characterized trees. We used the individual fruit production of baobab tree to calculate the mean fruit production of trees per study site. To assess age influence on the fruit production in African baobab in the studied localities we examined the relationship between fruit production and diameter at breast height.

2.3 Data analysis

Data collected in the three climatic zones were used to calculate the mean values per site. These mean values were compared using Kruskal-Wallis One way ANOVA. When statistical significant differences were detected, data series were compared pairwise with t-tests (when a normality test was passed) or the Mann-Whitney Rank Sum Test (when a normality test failed). All analyses were done in SigmatStat 3.5 and graphics were constructed in Excel 2008.

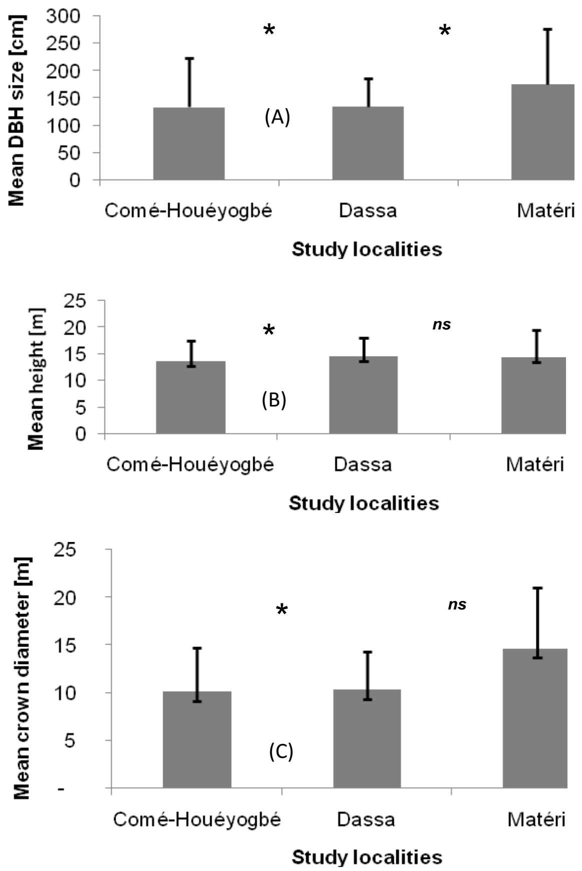

Figure 3. DBH size (A), tree height (B) and crown diameter (C) distributed in baobab populations at Comé-Houéyogbé, Dassa and Matéri districts. Significant differences between sites are indicated with with a star, ns for not significant (DBH: Kruskal-Wallis One way ANOVA, Tree height and Crown diameter: Mann-Whitney Rank Sum Test).

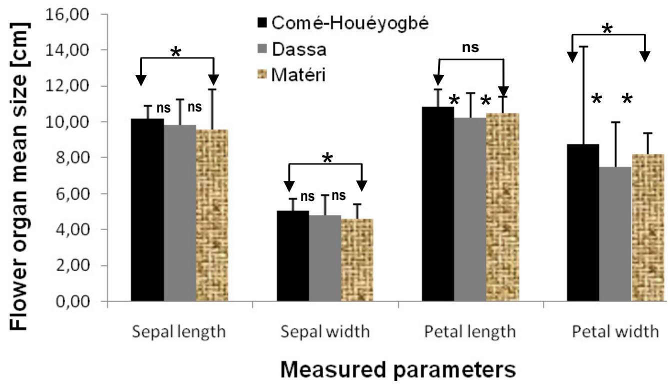

Figure 4. Comparison of flower organ size between studied sites. Significant differences between sites indicated with a star, ns for not significant (Kruskal-Wallis One way ANOVA, and Mann-Whitney U Statistic for pairwise comparison).

3 Results and discussion

3.1 Baobab population characterization

A total of 658 baobab trees in the three studied localities were characterized for size class (DBH), tree height and tree crown diameter (*figure 3*). Numbers of characterized trees per locality are as follows: Comé-Houéyogbé district (244) in the southwestern region, Dassa district (251) in the central region and Matéri district (163) in the extreme northwest of the country. The mean values of tree DBH, tree height and tree crown diameter show that the baobab trees tend to increase in size from the South (Comé-Houéyogbé) through the Center (Dassa) to the North (Matéri) of the country.

From the present study, it was observed that African baobab trees tend to be progressively larger moving from the Southern site, under Guinean climatic conditions, through the Central region with a Sudano-Guinean climate, to the Northern region with a Sudanian climate. This pattern might be explained by the fact that African baobabs meet their ecological optimum in the Sudanian zone. However, with just one population from each of the three zones, the differences observed could reflect local site histories such as differences in time of colonization. Indeed, the pattern detected, while showing similar north-to-south trends in DBH and crown diameter as those reported by Assogbadjo *et al.* [20], also showed greater tree height in Northern populations, contrary to [20].

3.2 Flower organ sizes in African baobab at the studied sites

The flower organs (sepals and petals) characterized in each site were compared among populations (*figure 4*). The size of the sepals and petals of flowers showed some statistically significantly differences among the studied localities. While comparing the sepal length, a statistically significant difference was detected between Comé-Houéyogbé and Matéri, but no statistical differences were found between Comé-Houéyogbé and Dassa or between Dassa and Matéri. A similar pattern was detected for sepal width. Flower petal width was significantly different from one site to another and quite a similar pattern was detected for petal length except between Comé-Houéyogbé and Matéri.

Flower organs differed in size by less that 10% among sites, so their observed differences seem insufficient to be a major determinant of flower visitation patterns among sites, specifically the lower flower visitation rate in Dassa compared with the other sites. Differences in the flower visitation rate could be due to food (nectar and pollen), which might vary among sites. [21, 22] reported that soil fertility and moisture affect rates of nectar production. Thus, the Dassa region might be expected to produce "poor" nectar, which could explain the low visitation rates by flying foxes [23, 24]. This is consistent with recent studies showing that the nectar volume increases the visitation rate of pollinators including bats [23,25] and data showing that at least flower visiting neotropical bats can have a well-developed perception and discrimination of volumes of nectar [26, 27]. Combined with the excellent spatial memories of pteropodids, which can allow them to relocate plants they have visited previously [26], nectar quality could have a direct effect on the visitation rate. On the other hand, it is also possible that the flying fox abundance at the Dassa site is low and this explains the low visit rate. It is likely that insufficiently

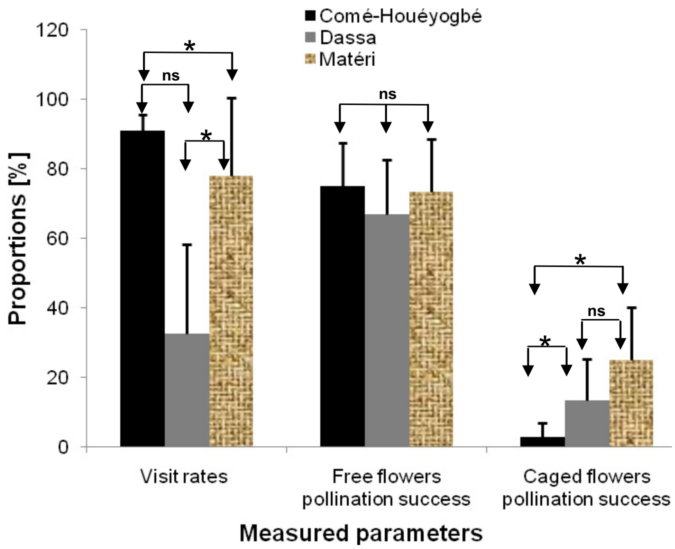

Figure 5. Pollinators visits and pollination success on baobab flowers. Significant differences between sites indicated with a star, ns for not significant (Kruskal-Wallis One way ANOVA, and Mann-Whitney U Statistic for comparison two by two).

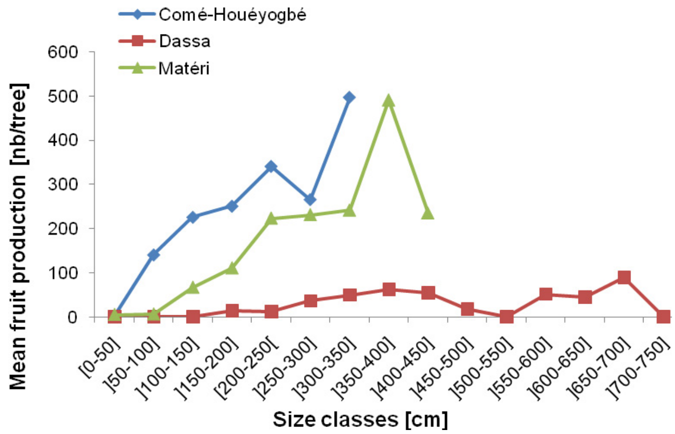

Figure 6. Fruit production per size classes in studied localities. No significant differences (Kruskall-Wallis One way ANOVA, H = 0.460; df = 2; p = 0.794).

pollinated flowers would be more likely to abort [28], thus explaining the low level of fruit set in caged flowers.

3.3 Flower visits and pollination success

The calculated visitation rates and the pollination success on free and caged flowers during the study period are shown as follows (*figure 5*). The highest visitation rate was recorded in Comé-Houéyogbé (91%) in the southern region, followed by Matéri (78%) in the northern region, and the lowest in Dassa (32.5%) in the central region. For pollination success on free flowers, no significant differences were detected among sites, but significant differences were detected for caged flowers, specifically between Comé-Houéyogbé *vs.* Dassa and Comé-Houéyogbé *vs.* Matéri.

One puzzling aspect in our study was similar pollination success rates in different populations despite significant differences in visitation rates. With an apparently similar pollination success on the free (non-caged) flowers at all studied sites one might expect that visitation rates in Dassa should be similar to the other populations, instead of much lower as we observed. The pollination success is the percentage of visited flowers that bear fruit out of the total number of visited flowers. Recent studies in the new world in two orchids (*Satyrium longicauda* and *Changnienia amoena*) reported that pollination success was independent of both the population size of pollinators and density of plants [29]; and Johnson *et al.* [30] argued that pollen receipt may not only be a function of the number of times pollinators visit flowers but also a function of pollinator efficiency. Engel and Irwin [31] defined the pollinator efficiency as the stigma pollen load deposited per pollinator visit. This suggests that flying foxes which visited baobab flowers in Matéri, where the highest visit rate was reported, were not efficient enough in pollen grain deposition to result in a different pollination success from the other sites. And the pollinators of Dassa showed apparent good efficiency to result in a quite similar pollination success, although its visitation rate was the lowest.

The pollination success of opened flowers was noticeably greater than that of caged flowers. This result confirms that bats play a key role in the pollination success of baobab, at least in terms of fruit production. The limited pollination success recorded in caged flowers is likely due to self-pollination, induced by the hemaphroditism of *Adansonia digitata* flowers, but also could reflect cross-pollination by insects, most likely dominated by the sphingid moth species that we saw active at night on baobab flowers. We consider wind-pollination unlikely discounted by a previous study [6].

3.4 Fruit production of baobab trees in Benin

Fruit production distributed into size classes (*figure 6*) is presented to show the contribution of DBH classes (a likely proxy for age) to fruit production in each population.

The pollination success reported in this early stage of the fruiting process (2–8 weeks after flower visit/laceration) is quite high and may not reflect ultimate fecundity because some of these fruits will abort before maturation, which takes about 5 months [34].

Fruit production per tree was different among sites, with the Dassa region showing the lowest fruit production. Since the pollination success of opened flowers was not different in the studied sites, fruit production of baobab should also be similar. The difference observed in Dassa is related to the number of flowers that were efficiently pollinated because the number of flowers that showed apparent visible visitation traces didn't really bear fruits ending up with a low number of fruits produced. The efficacy of the pollination syndrome in this region should therefore be questioned. At this stage of research, we can point out the pollination service is likely to be a major factor for fruit production problems in African baobab in the Dassa region, but some details are still missing to fully conclude. Probably local environmental conditions also play some role.

4 Conclusion

Our data suggest that the baobab has obligatory needs for the intervention of pollinators, namely fruit bats to reach its optimal pollination success. Flower characteristics such as night-blooming, abundant nectar production, large flowers, white petals, and strong odor are associated with the chiropterophilous syndrome [32, 33]. The exserted stigma, often widely separated from the stamens, demonstrates the clear need for relatively large animals that could transport pollen to the tip of the stigma.

The involvement of fruit bats that travel long distances in the pollination of baobab is beneficial as it may help conserve the genetic diversity of this plant species, a multipurpose socioeconomically relevant plant for Sub-Saharan African rural communities.

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