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Floral morphology and pollination system of *Syzygium guineense* (Willd.) DC. subsp. *macrocarpum* (Engl.) F. White (Myrtaceae), a subspecies with high nectar production

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ABSTRACT

The floral morphology and pollination of *S. guineense* subsp. *macrocarpum* were investigated on ten trees selected for a study of floral phenophases in the natural forest of Bassila, located in the Sudano-Guinean zone (Benin). For the floral analysis, the two stages considered were flower buds for preflowering data and open flowers for flower data. To determine the pollination mode and identify main pollinators, two stages were considered, namely flower bud and initiated fruits. The fruit set, autogamy and allogamy rate were assessed. Results show that several flower morphological traits predispose this species to selfing and cross pollination, including hermaphroditism and a long anther–stigma distance. The symmetry is actinomorphic with a floral receptacle adnate to the ovary. The latter is inferior, bicarpellary and bilocular syncarpous and contains 18–22 ovules on an axile placenta. Only a single ovule is fertilized and becomes a seed. Visitors frequently registered on the flowers of *S. guineense* subsp. *macrocarpum* are exclusively insects belonging to six orders, including Diptera (26%), Hymenoptera (24%), Lepidoptera (19%). The mean fruit set was 0.47 ± 0.10 for the open-pollination experiments and 0.27 ± 0.12 for autogamous self-pollination. The autogamy rate was 57.45% and the allogamy rate 42.55%. This study confirms that *S. guineense* subsp. *macrocarpum* is predominantly autogamous. Self-compatibility is not for exceptional species, but a dominant characteristic of the genus *Syzygium*. The viability of the pollen grains and receptivity of the stigma at each flowering stage should be further studied.

1. Introduction

Reproductive morphology, especially the type of breeding system in plants is important for the taxonomic classification of Angiosperms. Thus, the identification and easy recognition of plant species depend on reproductive traits while fruit and seed set result from successful pollination, pollen loads and nectar reward. Many plants are capable of reproduction via sexual and asexual means. In order to successfully reproduce sexually, plants have evolved specialized floral structures, many of which promote out-crossing, driven by the benefits associated with genetic diversity (Mayer et al., 2011). Studies on reproductive ecology include various topics such as pollination biology, floral biology, breeding systems, incompatibility reactions and phenology (Gibbs, 1990; Kearns and Inouye, 1993). About 20% of all Angiosperm families include plant species for which pollen transport does not rely on animal vectors, but which depend on physical agents such as wind and water for pollen transfer (Ackerman, 2000). Nevertheless, animal pollination is essential for the reproduction of the majority of plant species. Many wild flowers and crop plants depend on insects as pollinators to set seed. The pollen-ovule ratio thereby is an important floral trait characterizing the mating system of a plant (Cruden, 1977; Bennett, 2001; Bosch et al., 2001; Jürgens et al., 2002).

The taxon Myrtaceae belongs to the order Myrtales (APG IV, 2016). It has a wide distribution in tropical and warm temperate regions of the world and is typically common in some of the world's biodiversity hotspots. The genus *Syzygium* Gaertn. is regarded as one of the largest genera of flowering plants. It has a worldwide distribution in tropical and subtropical regions and is known from many regions including South Africa, South America, South East Asia and Australia. *Syzygium* species are characterized by caduc petals, terminal or sometimes lateral inflorescences that are cymes, independent cotyledons in fruit reported as a drupe (Akoegninou et al., 2006).

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A reproductive ecological study of a *Syzygium* species indicated that both self-compatibility and self-incompatibility exist in this genus with self-compatibility being most common (Sanewski, 2010).

Syzygium guineense (Willd.) DC. is a tree of 10 to 15 m high, with a thick and tortuous bole, generally low branching, with a fairly dense crown and drooping branches (Arbonnier, 2008). It has a mixed system of sexual reproduction (allogamous and self-pollinated); pollination is essential for the massive fruiting of this species (Djonwangwe et al., 2011). The plant has entomophilous pollination; moreover it can cross with neighboring *Syzygium* species (Orwa et al., 2009).

Syzygium guineense subsp. *macrocarpum* (Engl.) F.White is a synonym of *Syzygium pratense* Byng (WCSP, 2020). It has terminal and lateral inflorescences at the top of often defoliated branches; leaves are obovate-elliptic to broadly elliptic, coriaceous with a system of veins highly salient below, and a long petiole; fruits are globose, up to 3 cm in diameter (Akoegninou et al., 2006). Within this subspecies, polymorphism of fruit at maturity based on color is observed (Lamy Lamy et al., 2018). In apiculture, its nectar production has been evaluated at 8 μl per flower per hour, either 23.72 l per hectare and per day (Yedomonhan, 2009). Then *Syzygium guineense* subsp. *macrocarpum* acts as the most important nectariferous plant species in the Sudano-Guinean transition zone in Benin visited by bees for the accumulation of honey in hives (Yedomonhan, 2009). According to Djonwangwe et al. (2011), the rate of bee visits is positively correlated with the flowering rate of this Myrtaceae with a number of 256 bees per 1000 flowers. These studies reported only *Apis mellifera adansonii* Latreille as pollinator. Unfortunately, conservation of *Syzygium guineense* subsp. *macrocarpum* for boosting the apiculture development in Benin are constrained by many factors. Firstly, (Badou et al., 2017a) reported the recalcitrance of these seeds. This could be explained the scarcity of its regeneration and rarety of its adult individuals (Badou, 2017). In this context, assisted regeneration could facilitate its easy multiplication and its restoration in its natural habitats. Secondly, a full floral analysis of *Syzygium guineense* is not available for Benin nor elsewhere. This is however, important for understanding reproductive traits in order to master the strategies for seedlings. Thirdly, the species is subjected to overexploitation for charcoal, thus reducing the potential sources of nectar. The purpose of this study is to characterize the floral morphology of which traits directly influence reproductive success, together with the pollinators and the pollination pattern related to this subspecies.

2. Material and methods

2.1. Study area

The study was conducted in the natural protected forest of Bassila located in Sudano-Guinean zone. With an area of 2250 ha, this forest was subjected to classification under no. 2843 on August 5th, 1943 (DGEFC, 2016) and is located 375 km from Cotonou. It belongs to Bassila city. Mean temperature are high, hovering around 26 °C. The monthly minimums are between 20 °C in December and 24 °C in April. The monthly maximums vary from 29 °C in August to 38 °C in March (Badou, 2017). The climate is humid tropical transition type characterized by a dry season from mid-October to mid-April and a rainy season between mid-April and mid-October. Average annual rainfall is between 1200 and 1300 mm, making the Bassila district one of the wettest regions of Benin. Soils are of tropical ferruginous type. In terms of land use, population densities are low, between 12 and 20 inhabitants per km^2 (INSAE, 2016).

2.2. Data collecting

2.2.1. Floral analysis of S. guineense subsp. macrocarpum

Two stages of floral phenophases were considered: flower buds for preflowering data and flowers at anthesis for flower data (Badou et al., 2017b). For this purpose, 150 flower buds and 150 flowers at anthesis were collected from ten trees selected in the forest. Specifically, the floral analysis focused on type of inflorescence and number of flower per inflorecence, bracts, floral symmetry, flower sex after dissection to determine wether all flowers were hermaphroditic, as well as to document all floral cycles (protective or sterile for perianth, and fertile or reproducing for androecium and gynoecium) and their structure following dissections. Transversal and longitudinal sections of the ovaries were made to assess the organization of the ovules using a magnifying glass. Data were therefore based on qualitative morphological characters (shape, color, position, decay or not, welding or not, pre-blooming, nectariferous glands, etc.). These qualitative characteristics were supplemented by quantitative characters focusing on the number, length and diameter of floral parts and the floral traits cycles.

2.2.2. Identification of main pollinators and mode of pollination of S. guineense subsp. macrocarpum

For the inventory of pollinator, a group of three inflorescences was randomly chosen per selected tree. The observations were conducted for 10 min each time, at 6 a.m., 9 a.m., 12 a.m., 3 p.m. and 6 p.m. for each tree, according to the method applied by Ewedje et al. (2015). The types of visitors, the number of visits per flower, the duration of each visit and floral rewards (nectar and / or pollen) exploited by visitors were recorded. Visitors were captured using a net (a tool made from a cloth fabric, mounted on a circular wire attached to a wooden handle) as advocated by Goldingaye et al. (1991). After capture, each insect was kept in 70° alcohol, with date, time of capture and sample number for identification. The collection period covered the entire flowering phase from December to February (Badou et al., 2017b), 50 minutes of observation were made per day.

To assess the mode of pollination, especially to check if this plant species is self-pollinating, two groups of three inflorescences per treatment, exclusively in the flower buds stage were selected for each of the ten trees. The first considered stage is that of flower buds and the last concerns initiated fruits (Badou et al., 2017b). Inflorescences were marked with paint and underwent different treatments according to the type of pollination trials:

- autogamous self-pollination treatment: flower buds were covered with a white transparent fabric, as recommended by Kearns and Inouye (1993), to prevent their visit by pollinators.
- control without treatment: open pollination i.e. free exposure of flower buds that can be visited by the usual pollinators; here, all types of pollination are possible.

Follow-up was twice per week and flower buds that evolved to initiated fruits were counted per inflorescence.

2.3. Data processing

The floral morphology and the structure of flower parts such as androecium and gynoecium were illustrated using annotated drawings of longitudinal sections of flowers along with the floral diagram. Average number of ovules per ovary was determined by dissecting the ovaries under a microscope and the ovule/seed ratio was determined.

The relative incidence of insects was expressed in percentage. The average mean number of insect visits and the average time of visits were calculated. Results were compared using analysis of variance (ANOVA). Normality of data was previously verified.

The fruit set (I_{fr}) was calculated using fraction [number of fruits formed/number of viable floral buds], following Tchuenguem Fohouo et al. (2001). It was determined per inflorescence and per tree and was used for the comparison of fruit sets. The allogamy rate was calculated using the formula: TC = [($I_{fr}X$ - $I_{fr}Y$) / $I_{fr}X$] x 100, where $I_{fr}X$ and $I_{fr}Y$ are the mean fruit set of inflorescences without treatment and autogamy treatment respectively (Demarly, 1977). The autogamy rate was calculated by formula: TA = 100 - TC, whereby TA is the autogamy rate and TC allogamy rate.

3. Results

3.1. Inflorescence and floral morphology of S. guineense subsp. macrocarpum

Table 1 and Fig. 1 show the flower morphology. The inflorescence of *S. guineense* subsp. *macrocarpum* is a composite cymose or thyrse (cluster of cymes). The number of inflorescences per tree ranges from 168 to 945, each inflorescence produces 19–118 flowers. The actinomorphic flowers are predominantly white, complete, hermaphroditic, cyclic, with pedicels covered with small triangular deciduous bracts. Despite hermaphroditism, flower displayed a relatively high anther-stigma distance (Fig. 1A,D). The floral receptacle (hypanthium) is adnate to the ovary. Flower buds were conical or obconical, red or light green at the apex before anthesis. At anthesis, the flower acquires an average length of 15.10 ± 0.88 mm and a width of 6.05 ± 0.51 mm at the reference level of floral receptacle.

The calyx consist of four sepals surmounted by four teeth or lobes welded regularly into a cone or are funnel-shaped adnate to the ovary. The width of the sepals is 2.33 to 3.29 mm (mean ± sd = 3 ± 0.19 mm). The length varies from 7.13 to 8.53 mm (mean ± sd = 7.47 ± 0.52 mm). The corolla comprises four to five imbricate and deciduous petals (Fig. 1A). Petal width is 3.18–4.56 mm (mean ± sd = 3.87 ± 0.69 mm) while it long from 3.19 to 4.84 mm (mean ± sd = 4.17 ± 0.67 mm).

The androecium contained 119 to 157 stamens inserted around the mouth of the calyx tube (Fig. 1B,D). Stamens are composed of white filaments and yellow anthers with 2 pollinic lodges. Anthers dehisc longitudinaly. The length of filament is 3.37–7.57 mm (mean ± sd = 5.02 ± 0.54 mm) while anthers length varies from 0.38 to 0.51 mm (mean ± sd = 0.43 ± 0.10 mm). In the gynoecium, ovary is infer (Fig. 1A), bicarpellary and bilocular syncarpous displaying an axile placentation and harboring 18-22 ovules. Only a single ovule matures to seed within each ovary, giving an average ovule/seed ratio of 5%. The ovary length varies from 1.8 to 3.52 mm (mean ± sd = 3.08 ± 0.56 mm). The style is white with a simple stigma arising from the center of the cup and almost hidden by stamens (fig. 1A), with a length of 3.83 to 7.49 mm (mean ± sd = 5.20 ± 0.37 mm). The yellowish nectariferous gland is clearly visible inside the floral receptacle (Fig. 1D).

3.2. Flower visits, pollination system and fruit set

Visitors frequently recorded on the flowers of *S. guineense* subsp. *macrocarpum* were exclusively insects belonging to six orders including Diptera (26%), Hymenoptera (24%), Lepidoptera (19%), Orthoptera (11%), Coleoptera (10%) and Hemiptera (7%). However, spiders and mites were also recorded but represented only 3% of the inventory. Indeed, Diptera, Hymenoptera and Lepidoptera were the predominant insects (69%). Diptera was mainly represented by *Musca domestica* Linnaeus and were more abundant than all other visitors with one to six visits per minute. The average duration of a Dipteran visit ranged from 1.5 to 3.23 sec. mostly for pollen harvest (Table 2). As for Hymenoptera, they were mainly represented by *Apis mellifera adansonii* Latreille (Fig. 1C) with one to two visits per min mostly for nectar harvest. Hymenoptera spent more time per flower than all other visitors and the average time of a visit ranged from 7.5 to 17.5 sec. Lepidoptera were mainly represented by *Abantis bismarcki* Karsch. The average duration of a Lepidopteran visit ranged from 1.5 to 5.15 sec. with one to two visits per min. mostly for pollen harvest. Visit duration varied significantly according to the orders of insects (p-value = 0.000). Intense foraging activity was recorded mainly from 12 a.m. to 3 p.m. for all insects (Table 2).

Fruit set varied from 0.39 to 0.61 for open-pollination (Fig. 2A) and was higher than 0.10–0.38 for autogamous self-pollination (Fig. 2B). A mean fruit set of 0.47 ± 0.10 for open-pollination and 0.27 ± 0.12 for manual autogamous self-pollination was registered. The autogamy rate was 24.54 to 77.89% with a mean of 57.45% while allogamy rate was 42.55%. Consequently *S. guineense* subsp. *macrocarpum* ha a predominantly autogamous pollination.

4. Discussion

4.1. Floral analysis of S. guineense subsp. macrocarpum

Floral symmetry has a relevant status in the study of both pollination systems and pollinators' behavior (Giurfa et al., 1999). The floral parts and floral formula are very important for a correct identification of Angiosperm plants. Shape, size and finer details of different parts of a flower are needed to identify a species. The actinomorphic flowers, the large receptacle where insects can land and the production of floral rewards indicate that *S. guineense* is attractive to visitors. Apart

Table 1
Qualitative and quantitative description of the reproductive apparatus of *S. guineense* subsp.*macrocarpum*

	Description	Number	Length (mm)	Width (mm)
Inflorescence	thyrse terminal, cluster of cymes.	[168 - 945] per tree	-	
Pedicel	present, short	only, by flower	[1.5- 2.5]	
Floral bract	caducous or deciduous, scaly.	-	-	
General characters of the flower	complete, bisexual hermaphrodite, cyclic or verticillate, actinomorphic, predominantly white because of stamens; floral receptacle (hypanthium) adnate to the ovary	[19 - 118] per inflorescence	15.10 ± 0.88	6.05 ± 0.51
Calyx	gamosepalous, green, persistent, funnel-shaped, adnate to the ovary, aestivation valvate, 4 teeth or lobes.	4 welded sepals	[7.13 - 8.53]	[2.33 – 3.29]
Corolla	caducous or deciduous, red or light green corolla, visible only from the top of the flower, imbricate aestivation.	[4 - 5] caducouspetals	[3.19 – 4.84]	[3.18 – 4.56]
Androecium	dialystemonous, 1 cycle of numerous stamens inserted around the mouth of the calyx tube; white filaments; yellow anthers, introrse, dithecous, dehiscence by longitudinal slit	[119 - 157] (stamens)	[3.37 – 7.57] (filaments)	[0.38 – 0.51] (anthers)
Gynoecium or pistil	Epigynous, syncarpous, 2-celled ovary, axile placentation, anatropic hanging ovule; style and stigma simple, linear, white and almost hidden by stamens, yellowish nectariferous gland.	[18 - 22] (ovules)	[3.83 – 7.49] (stylum)	[1.8- 3.52] (ovary)

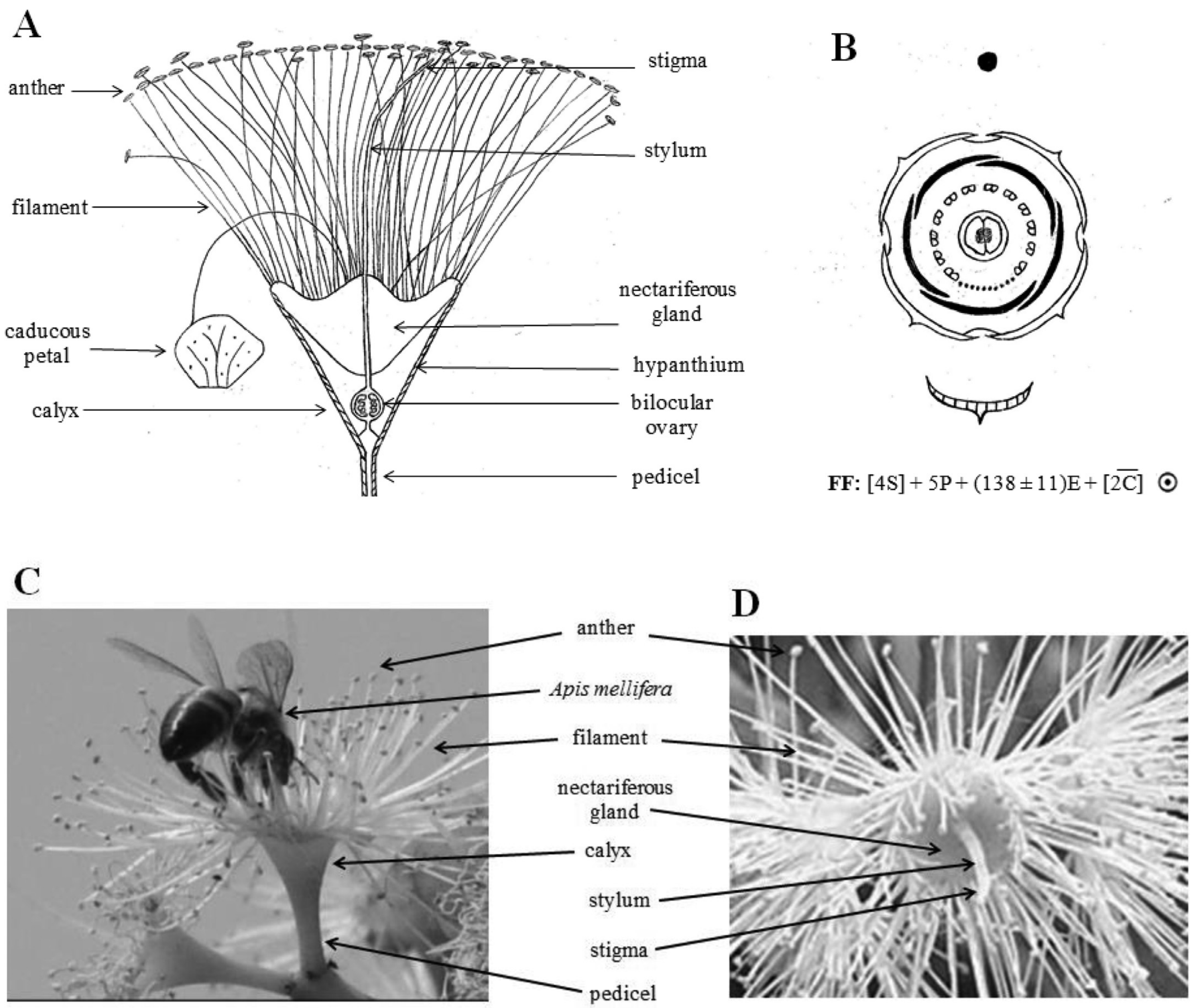

Fig. 1. Some morphological characters of *S. guineense* subsp.*macrocarpum*: **A**. Longitudinal section of flower. **B**. Floral diagram and formula; **C**. Harvest of nectar on the flower by *Apis mellifera*; **D**.Detail of a flower showing the nectariferous gland.

Table 2
Major visitors to flowers of *S. guineense* subsp. *macrocarpum*.

Order and family of prominent insects	Visits	6 a.m.	9 a.m.	12 a.m.	3 p.m.	6 p.m.	Nutrients collected
DIPTERA Muscidae (91%), Syrphidae (9%)	Average length of a visit (s)	1.5 ± 1.08	2.5 ± 2.47	3.23 ± 2.56	3 ± 2.24	2.25 ± 2.09	pollen (80%), nectar (20%)
	Average number of visits / min	1 ± 1	2 ± 1	3 ± 2	3 ± 2	1 ± 1	
HYMENOPTERA Apidae (74%), Vespidae (18%), Formicidae (8%)	Average length of a visit (s)	0	7.5 ± 5.61	15 ± 11.22	17.5 ± 7.68	9.5 ± 9.23	pollen (33%), nectar (67%)
	Average number of visits / min	0	1 ± 1	1 ± 1	1 ± 1	1 ± 1	
LEPIDOPTERA Hesperiidae (61%), Lycaenidae (39%)	Average length of a visit (s)	0	4.52 ± 2.88	5.15 ± 3.63	5.13 ± 2.42	1.5 ± 1.12	pollen (57%), nectar (43%)
	Average number of visits / min	0	1 ± 0	1 ± 1	1 ± 1	1 ± 0	

from selfing promoted by hermaphroditism, the long anther-stigma distance predispose this subspecies to cross pollination.

With regard to morphological traits of *S. guineense* flowers, some authors have found similar results on *Syzygium aromaticum* L. (Clove) (Kaur and Chandrul, 2017), *S. hookeri* M.V. Ramana, *S. sanjappaiana* M.V. Ramana (Ramana et al., 2014), *S. fratris, S. glenum, S. monimioides* and *S. monospermum* (Craven, 2003).

The mean rate of unfertilized ovules per flower of *S. guineense* subsp. *macrocarpum* was high in this study. Similar results have been described in other plant species (Schemske and Horvitz, 1988, Ley, 2008) and seems to be a general characteristic of Angiosperms. This could be explained by an insufficient pollinator visitation rate, pollen loss during transport by pollinators, floral resource limitation and/or low pollen viability. In Myrtaceae species, the ovary usually contains more ovules but few succeed to be fertilized, evolve and form seed. For example, abortion of ovules in *Syzygium cuminii* is substantiated by experimental work in which the extracts from the dominant seeds, containing predominately indole compounds, inhibited

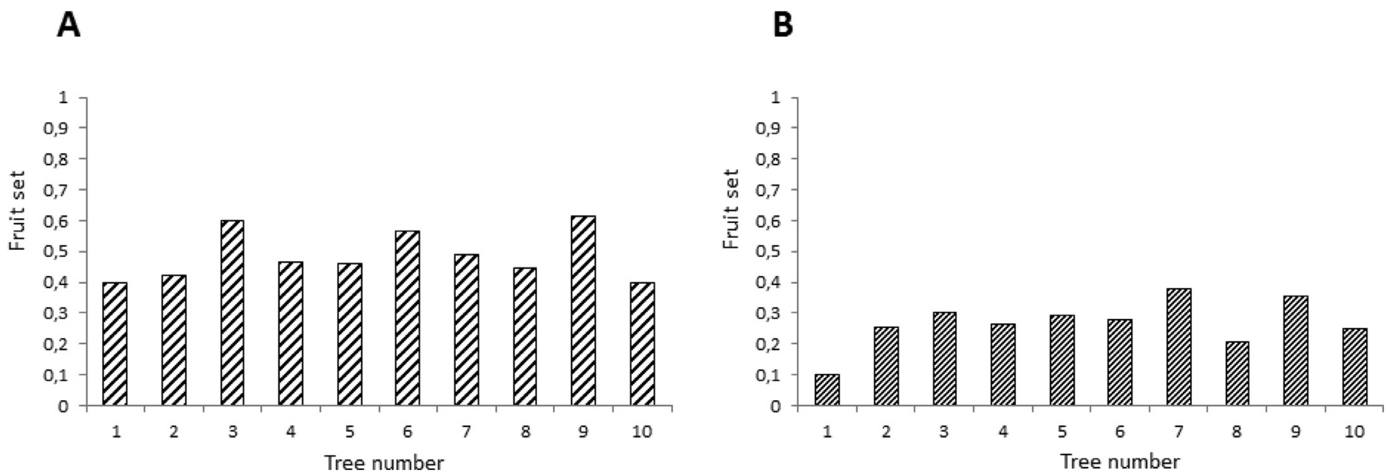

Fig. 2. Fruit set per tree: **A.** Open-pollination; **B.** Autogamous self-pollination

resource uptake by the sub-ordinate seeds. The plant therefore usually developped only one mature ovule (Chantaranothai and Parnell, 1994; Lughadha and Proenca, 1996; Arathi et al., 1996; Krishnamurthy et al., 1997; Kader et al., 2000; Khan et al., 1995). Such a situation can be expected in its allied species *S. guineense* subsp. *macrocarpum* in which also only one ovule forms a seed per fruit, the others being aborted.

4.2. Pollinators and pollination system analysis

This study revealed the high abundance of insects from 12 a.m. to 3 p.m. This fact is justified by the high amount of nectar rich in sucrose sugar and protein during this period (Yedomonhan, 2009). The long duration of visits of *A. mellifera adansonii* compared to other insects can be explained by the foraging strategy of the bees, which consists to move from one flower to another within the same inflorescence, spend more time per flower and visited more flowers per inflorescence, thus promoting selfing (Ewedje et al., 2015). A diversity of insect foragers benefit highly from the flowering season of *S. guineense*. In Africa and in Benin, *S. guineense* is reported to be a honeybee plant but details of pollination are lacking. The present study shows that among this species pollinators, flies, bees and butterflies are predominant. In Australia, blossom bats and honeyeaters are primary pollinators of *S. sayeri*, although butterflies, flies, thrips and wasps also play a role in pollination (Williams and Adam, 2010).

This study also revealed that *S. guineense* subsp. *macrocarpum* is a predominantly selfing plant in contrast to mixed pollination with the predominance of allogamy for *S. guineense* subsp. *guineense* in Cameroon (Djonwangwe et al., 2011). This difference within the same species can be explained mainly by the strategy of collection method, but also by the ecological conditions of the study area. The present study shows that *S. guineense* subsp. *macrocarpum* is self-compatible, as is common for many other *Syzygium* species (Raju et al., 2014; Sanewski, 2010; Reddi and Rangaiah, 2000; Stacey, 2001).

The duration of pollen viability and stigma receptivity are critical for many reasons (Dafni et al., 2005). This is the first step before a pollen grain can germinate in the case of cross pollination treatment. This pollen-stigma relationship depends on pollen viability, stigmatic receptivity, and genetic interaction and may vary according to environmental conditions such as relative humidity or temperature (Franchi et al., 2007; Douglas and Freyre, 2010).

5. Conclusion

This study revealed that *S. guineense* subsp. *macrocarpum* is a bisexual plant that benefits from the pollination by insects among which the families Muscidae and Apidae are the most important. The mean fruit set is high under open-pollination and the autogamy rate is higher than the one for allogamy. The viability of pollen grains and stigma receptivity at each flowering stage deserve to be further studied. Finally, *S. guineense* should be planted and protected to increase honey production.

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Authors' contributions

RBB, HY, EEBKE and AA conceived, and designed the research. RBB collected the data and wrote the manuscript. HY, ACA, MGT and HGD analyzed the data. All authors read and approved the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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References

Ackerman, J.D., 2000. Abiotic pollen and pollination: Ecological, functional, and evolutionary perspectives. Plant Systematics and Evolution 222, 167–185.
Akoegninou, A., van der Burg, W.J., van der Maesen, L.J.G., 2006. Flore Analytique du Bénin. Backhuys Publishers, Wageningen.
APG, IV, 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV (PDF). Botanical Journal of the Linnean Society 181 (1), 1–20.
Arathi, H.S., Ganeshaiah, K.N., Shaanker, R.U., Hegde, S.G., 1996. Factors affecting embryo abortion in *Syzygium cumini*(L.) Skeels (Myrtaceae). International Journal of Plant Sciences 157, 49–52.
Arbonnier, P.B.M., 2008. Ligneux du Sahel. Outil Graphique D'identification V.1.0. CIRAD.
Badou, B.R., 2017. Ethnobotanique, Écologie et Phénologie de la Reproduction Sexuée de Syzygium Guineense (Willd.) DC. subsp. Macrocarpum (Engl.) F. White

(Myrtaceae) en zone Soudano-guinéenne (Bénin). These de Doctorat de l'Université d'Abomey-Calavi (Bénin.
Badou, B.R., Yedomonhan, H., Adomou, A.C., Akoegninou, A., 2017b. Phénologie florale et production fruitière de *Syzygium guineense* (Willd.) DC. subsp. *macrocarpum* (Engl.) F. White (Myrtaceae) en zone soudano-guinéenne au Bénin. International Journal of Biological and Chemical Sciences 11 (5), 2466–2480.
Badou, B.R., Yedomonhan, H., Ewedje, E.-E., Guezodje, G., 2017a. Dehydration capacity and germination of the generative seeds of *Syzygium guineense* (Willd.) DC. subsp. *macrocarpum* (Myrtaceae) in Benin. International Journal of Advanced Research in Biological Sciences 4 (10), 95–104.
Bennett, S.J., 2001. Pollen−ovule ratios as a method of estimating breeding system in *Trifolium* pasture species. In: Proceedings of the 10th Australian Agronomy Conference, Hobart. available at http://www.regional.org.au/au/asa/2001/6/a/bennett.htm).
Bosch, M., Simon, J., Molero, J., Blanche, C., 2001. Breeding systems in tribe Delphinieae (Ranunculaceae) in the western Mediterranean area. Flora 196, 101–113.
Chantaranothai, P., Parnell, J.A.N., 1994. The breeding biology of some Thai *Syzygium*-species. Tropical Ecology 35 (2), 199–208.
Craven, L.A., 2003. Four new species of *Syzygium* (Myrtaceae) from Australia. Blumea 48 (3), 479–488.
Cruden, R.W., 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31, 32–46.
Dafni, A., Nepi, M., Pacini, E., 2005. Pollen and stigma biology. Practical Pollination Biology. Enviroquest Ltd., Cambridge, Ontario, Canada, pp. 83–146.
Demarly, Y., 1977. Génétique et Amélioration des Plantes. Masson, Paris.
DGEFC (Direction Générale des Eaux, Forêts et Chasse), 2016. Annuaire des Statistiques Forestières. Programme de Gestion des Forêts et Terroirs Riverains / Ministère du Cadre de Vie et du Développement Durable. Cotonou (Rép. Bénin). http://dgfrn-bj.org.
Djonwangwe, D., TchuenguemFohouo, F.-N., Messi, J., Brückner, D., 2011. Foraging and pollination activities of *Apis mellifera adansonii* Latreille (Apidae) on *S. guineense* subsp. *guineense* (Myrtaceae) flowers at Ngaoundéré (Cameroon). Journal of Animal and Plant Sciences 10 (3), 1325–1333.
Douglas, A.C., Freyre, R., 2010. Floral development, stigma receptivity and pollen viability in eight Nolana (Solanaceae) species. Euphytica 174, 105–117.
Ewedje, E.-E.B.K., Ahanchede, A., Hardy, O.J., Ley, A.C., 2015. Reproductive biology of *Pentadesma butyracea* (Clusiaceae), source of a valuable non timber forest product in Benin. Plant Ecology and Evolution 148 (2), 213–228.
Franchi, G.G., Nepi, M., Matthews, M.L., Pacini, E., 2007. Antheropening, pollen biology and stigma receptivity in the long blooming species, Parietaria judaica L. (Urticaceae). Flora 202, 118–127.
Gibbs, P.E., 1990. Self-incompatibility in flowering plants: a neotropical perspective. Revista Brasileira de Botânica 13, 125–136.
Giurfa, M., Dafni, A., Neal, P.R., 1999. Floral symmetry and its role in plant-pollinator systems. International Journal of Plant Sciences 160 (6 Suppl.), S41–S50.
Goldingaye, R.L., Carthew, S.M., Whelan, R.J., 1991. The importance of non-flying mammals in pollination. Oikos 61, 79–89.
INSAE (Institut National de la Statistique et de l'Analyse Economique), 2016. Cahier des Villages et Quartiers de ville du departement de la Donga (RGPH-4, 2013). Ministère du Plan et du Développement, République du Bénin.
Jürgens, A., Witt, T., Gottsberger, G., 2002. Pollen grain numbers, ovule numbers and pollen−ovule ratios in Caryophylloideae: correlation with breeding system, pollination, life form, style number, and sexual system. Sexual Plant Reproduction 14, 279–289.
Kader, S.A., Bindu, K.R., Chacko, K.C., 2000. Polyembryony in *Syzygium cumini* (L.) Skeels and in *Vateria indica* L. Indian Forester 126, 1353–1356.
Kaur, D., Chandrul, K.K., 2017. *Syzygium aromaticum* L. (Clove): a vital herbal drug used in periodontal disease. Indian Journal of Pharmaceutical and Biological Research 5 (2), 45–51.
Kearns, C.A., Inouye, D.W., 1993. Techniques for Pollination Biologists. University Press Colorado, Niwot Ridge, CO.
Khan, P.S., Sudarsanam, G., Rao, K.R., 1995. Polyembryony and in vitro seed culture in *Syzygium alternifolium* (Wight) Walp. Journal of Phytological Research 8, 119–122.
Krishnamurthy, K.S., Uma Shaanker, R., Ganeshaiah, K.N., 1997. Seed abortion in an animal dispersed species, *Syzgium cuminii* (L.) Skeels (Myrtaceae): the chemical basis. Current Science 73, 869–873.
Lamy Lamy, G.M., Ibrahima, A., Ndjonka, D., Mapongmetsem, P.M., 2018. Etude ethnobotanique des sous-variétés de *Syzygiumguineense* (Will.) DC. var. *macrocarpum* (Engl.) F. White dans les Hautes Savanes Guinéennes (Adamaoua, Cameroun). International Journal of Biological and Chemical Sciences 12 (4), 1636–1649.
Ley, A.C., 2008. Evolutionary Tendencies in African Marantaceae − Evidence from Floral Morphology, Ecology and Phylogeny. Institut für Spezielle Botanik und Botanischer Garten University Mainz, Germany Ph.D. thesis.
Lughadha, E.N., Proenca, C., 1996. A survey of the reproductive biology of the Myrtoideae (Myrtaceae). The Annals of the Missouri Botanical Garden 83, 480–503.
Mayer, C., Adler, L., Armbruster, W.S., Dafni, A., Eardley, C., Huang, S.-Q., Kevan, P.G., Ollerton, J., Packer, L., Ssymank, A., Stout, J.C., Potts, S.G., 2011. Pollination ecology in the 21st century: key questions forfuture research. Journal of Pollination Ecology 3 (2), 8–23.
Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Anthony, S., 2009. Agroforestree Database: a tree reference and selection guide version 4.0. *Syzygium guineense* Myrtaceae (Willd.). World Agroforestry Center, DCKenya.
Raju, A.J.S., Krishna, J.R., Chandra, P.H., 2014. Reproductive ecology of *Syzygium alternifolium* (Myrtaceae), an endemic and endangered tropical tree species in the southern Eastern Ghats of India. Journal of Threatened Taxa 6 (9), 6153–6171.
Ramana, V.M., Chorghe, A., Venu, P., 2014. Two new species of *Syzygium* (*Myrtaceae*) from Saddle Peak National Park, Andaman and Nicobar Islands, India. Blumea 59 (1), 42–48.
Reddi, E.U.B., Rangaiah, K., 2000. Breeding systems and pollinating agents of the Indian black berry, *Syzygium cuminii* (L) Skeels (Myrtaceae). Journal of Palynology 35-36, 117–128.
Sanewski, G.M., 2010. Understanding the Cropping Behavior of Riberry (*Syzygium luehmannii*). Union Offset Printing, Canberra RIRDC Publication No. 10/194.
Schemske, D.W., Horvitz, C.C., 1988. Plant-animal interactions and fruit production in a neotropical herb: a path analysis. Ecology 69, 1128–1137.
Stacey, E.A., 2001. Cross-fertility in two tropical tree species: evidence of inbreeding depression within population and genetic divergence among populations. American Journal of Botany 88, 1041–1051.
Tchuenguem Fohouo, F.-N., Messi, J., Pauly, A., 2001. Activité de Meliponula erythra sur les Fleurs de Dacryodes edulis et son Impact sur la Fructification. Fruits 56, 179–188.
WCSP, 2020. World checklist of selected plant families. Facilitated by the Royal Botanic Gardens. Kew. Published on the Internet. http://wcsp.science.kew.org/.
Williams, G., Adam, P., 2010. The Flowering of Australia's Rain Forests. CSIRO Publishing, Melbourne.
Yedomonhan, H, 2009. Plantes Mellifères et Potentialités de Production de Miel en zone Guinéenne et Soudano-guinéenne au Bénin. Thèse de Doctorat de l'Université d'Abomey-Calavi (Bénin), FAST/UAC.